Geometric Morphometric analysis of the Microtus M1 and its application to Early Middle Pleistocene in the UK.

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Abstract

Species of the genus *Microtus* are known to be some of the most rapidly evolving taxa during the Quaternary. Their remains are common in archaeological and palaeontological contexts and are frequently used in palaeoclimatic and habitat reconstructions as well as providing a key component of biostratigraphic dating models.

This study focused on the dental morphology of the lower M_1 in 6 species of *Microtus* found in the British early Middle Pleistocene. The study examined the potential for a new approach to gaining better resolution in biostratigraphic and palaeoclimatic reconstructions in this period, using Geometric Morphometric (GMM) analyses.

GMM analyses of modern samples of known origin found that it was possible to identify M1 teeth to species level with a high degree of statistical significance (<0.0001). The application of protocols developed on modern samples to those from the early Middle Pleistocene sites at Westbury sub-Mendip and Boxgrove suggested species identification on ancient material was also possible. Taxonomic revision of the extinct species *Microtus arvalinus* was suggested by their morphological similarity to both modern and ancient *M. agrestis* samples, not *M. arvalis* as has previously been suggested. Identification of a large morphological disparity between modern and early Middle Pleistocene examples of *M. subterraneus* also suggest a complex genetic history, which previously had not been identified.

Additionally, evidence for morphological differences linked to climate was found. Variation in morphology between stratigraphic levels was found to be relatively low in

most cases, even when samples were thought to be separated by a significant period of time.

These findings strongly support the use of GMM methods in determining *Microtus* remains to species level and suggest a strong potential for their use as palaeoclimatic and relative-dating proxies, requiring further research.

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I would also like to thank my fellow PhD students who have always provided support, friendship and on occasion, much needed perspective!

Finally, I would like to thank my family, especially my parents, grandparents and Meyrick Irving for their continued support and encouragement without which completing this thesis would not have been possible.

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CHAPTER 1
INTRODUCTION AND AIMS OF THE STUDY

1.1 INTRODUCTION

This study aims to explore the dental morphology of six species within the genus *Microtus* in the British early Middle Pleistocene, to gain further understanding of their taxonomy and species identification , and improve the use of Pleistocene *Microtus* remains for dating and palaeoenvironmental reconstructions. Remains of Microtine rodents are extremely common in many Pleistocene sediments and are found in a wide variety of depositional environments across Europe. These remains are of importance in the reconstruction of past environments and climates, and the establishment of the relative ages of particular localities through biostratigraphic analysis. Despite their significance, quantitative analysis of Microtine rodents has been hampered, because of a lack of systematic examination of geographic variation and other confounding factors.

The major aims of this study are to undertake a detailed analysis and comparison of *Microtus* remains from two key early Middle Pleistocene localities; Boxgrove and Westbury Sub-Mendip. Both sites have complex stratigraphic sequences and are believed to represent more than one climatic phase. This research aims to correlate the sequences at these two sites, which have been suggested to be similar in age (Schreve, 2001), through a comparison of changes in the Microtine assemblages.

The principal method used to analyse the dental remains will be Geometric Morphometrics (GMM), a suite of statistical methods designed for recording and analysing biological shape. These results will be compared to published data using biologically standard metric measurements. The use of Geometric Morphometrics in palaeontological research to answer questions relating to relationships between species, migrations, taxonomy and functional morphology is still a relatively new area of exploration. However, several published studies suggest great potential for the application of these techniques to palaeontological remains, including rodents. For example, Cucchi *et al*. (2002) and Killick (2005) used Geometric Morphometrics to track past migrations of house mouse and *Microtus arvalis* respectively, whereas Polly (2003) employed the technique in an attempt to date the time between major geographic differentiations in the dentition of marmots. (A more in-depth discussion of the current uses of Geometric Morphometric studies is included in section 1.3).

The key issues this thesis aims to address are:

i) As the application of Geometric Morphometrics to fossil material of this age and type is a relatively new approach, one of the most important aims of this study will be to evaluate the suitability of such methods to this type of material and to analyse what new information can be gained through the application of this technique, as compared with more traditional metric measurements.

ii) To aim to quantify the range of morphological variation within both fossil and modern populations, as well as the amount of geographical variation that is present between populations. This should allow the reconstruction

of palaeophylogeographies which will be compared with established molecular phylogenies.

iii) To develop a GMM protocol using modern species to create species identification criteria. Once these criteria have been established, they will be applied to remains from the early Middle Pleistocene fossil record, producing a methodological framework which can be used in other studies of similar material.

iv) Identification of taxonomic revisions in the fossil samples, where appropriate.

v) Data gained from this study should allow the revision of current - and development of new- biostratigraphic models using Microtine rodents for the dating of European Palaeolithic sites- particularly revision and correlation of the stratigraphic sequences at two important British early Middle Pleistocene sites, Westbury-sub-Mendip and Boxgrove.

vi) Use of the Microtine assemblages to evaluate climatic changes at Westbury and Boxgrove and the effect of palaeoclimatic change on *Microtus* morphology. (i.e.; increased or decreased inter-population variation or body size changes).

vii) The prevailing climate has been suggested to have an effect upon the morphology of *Microtus* species, with fossil *Microtus grafi* (Brunet-Lecomte *et al.*, 1992) specimens from warmer climatic periods exhibiting a less tilted Pitymoid rhombus than those from cooler climates (Montuire *et al.*, 2004). Therefore, there is potential to analyse and track climatic changes through analysis of *Microtus* teeth. One of the major aims of this project is to investigate the migrational history and effect of climatic fluctuations on *Microtus* in an attempt to understand the island history of the British Isles

This chapter aims to provide a literature review and background information on the chronology of the sites, the development of Geometric Morphometric techniques and the biology and behaviour of *Microtus* species, thus placing the aims and objectives of this thesis within their wider context. In-depth information on *Microtus* taxonomy and habitats, the specific methods used within this study and the stratigraphic sequences at Westbury and Boxgrove are contained within chapters 2, 3 and 4 respectively.

1.2 BOXGROVE AND WESTBURY SUB-MENDIP IN THE CONTEXT OF THE BRITISH AND EUROPEAN EARLY MIDDLE PLEISTOCENE

1.2.1- INTRODUCTION

The focus of this study is in evaluating the potential of Geometric Morphometric methods and the analysis of *Microtus* teeth to the early Middle Pleistocene sites of Boxgrove and Westbury sub-Mendip. The information provided within section 1.2

provides information on the stratigraphic framework and relative ages of these sites, which is essential to interpret the results gained in subsequent chapters.

The early Middle Pleistocene in Europe is not sharply defined, but begins at the Bruhnes-Matuyama boundary (c. 780 Kya) and ends prior to the Anglian cold stage (c. 450 Kya), spanning MIS phases 19-12 and encompassing several glacial/interglacial cycles. The early Middle Pleistocene is an important period within the prehistory of the British Isles as it saw first hominin occupation of Britain. Until recently the earliest evidence of occupation in the north west of Europe (including Britain) was thought to be in MIS 13 at the sites of Boxgrove (Roberts & Parfitt, 1999) and Westbury sub-Mendip. The site at Westbury is thought to date to MIS 13 or 15 (see discussion below; Andrews *et al.*, 1999) in Britain and is thought to be of a similar age to the earliest sites in Germany, Meisenheim and Mauer (Wymer, 1999; Dennell & Roebroeks, 1996). However, recent finds of worked lithics at Pakefield and Happisburgh, both on the Norfolk Coast, suggest that hominin occupation of north western Europe was significantly earlier, dating to MIS 17 or 19 (Parfitt *et al.*, 2010). This recent discovery serves to illustrate that despite in-depth study of the early Middle Pleistocene in Europe, our understanding of the period is far from complete and frequently changing.

Throughout the Pleistocene, climate and global sea levels changed rapidly. Britain was joined to the European mainland while sea levels were low, and cut off by the sea while sea levels were high. Prior to the breach of the Dover Strait (at or later the MIS 12), in the early Middle Pleistocene, Britain was permanently connected to the European mainland (Gibbard, 1995; White & Schreve, 2001). The rapid change in climate caused large fluctuations in the floral and faunal composition of the UK, resulting in rapid faunal turnover leading to distinctive groups of mammalian species.

As a result of the land bridge, the early Middle Pleistocene is an interesting period, both in terms of faunal and human migration and interaction with continental Europe. Sediments of this age are relatively uncommon and discontinuous in Britain, so reconstructing the sequence of sites and climatic change is complex; sites are few and far between and material is often sparse. This study focuses upon *Microtus* remains at two of the most important British early Middle Pleistocene sites; Boxgrove and Westbury Sub-Mendip. This section aims to introduce the early Middle Pleistocene context of both of these sites, in a British and European context.

1.2.2 THE LOWER MIDDLE PLEISTOCENE IN BRITAIN

The early Middle Pleistocene record within Britain is fragmentary and geographically disparate. There are several main sites which have been identified as being early Middle Pleistocene in age within the British Isles, as can be seen in figure 1.1. Explanation of their relative ages is discussed below.

The early Middle Pleistocene in Britain was a time of intense and rapid climate change. Oxygen Isotope analysis from air trapped in ancient ice cores has suggested the presence of several glacial and interglacial cycles within this time period, with associated sea-level changes (Bassinot *et al.*, 1994). Throughout the early Middle Pleistocene, when sea levels were low during cold periods, the North Sea was a terrestrial basin; during the Anglian glaciations (MIS 12) an ice-dammed lake in the south North Sea overflowed catastrophically, breaching the land-bridge and providing the geological conditions for island status during interglacial periods with sufficiently high sea-level (Smith, 1989; Gibbard, 1995; White and Schreve 2001; Gupta *et al.* 2007).

The early Middle Pleistocene in Britain is often referred to as the 'Cromerian', named after a series of sediments collectively known as the Cromer Forest bed Formation (CF-bF), which were the first sediments identified as being of early Middle Pleistocene in age within Britain (Preece & Parfitt, 2000). The CF-bF consists of a complex series of freshwater and marine sediments, discontinuously present for over 100 km across the North Sea coast of Norfolk and Suffolk, Britain. These deposits contain an abundance of preserved biological remains, including mammals, pollen and plant macrofossils, and Mollusca. The Cf-bF lies above the basal Early Pleistocene Westbourne Crag deposits and below the glaciogenic deposits attributed to the Anglian stage (410 Ky BP). The position of the Cf-bF sandwiched between these two deposits suggests the date of the sediments lies somewhere within the early Pleistocene to late Middle Pleistocene age range (Preece *et al.*, 2009).

The CF-bF deposits were originally discovered by Celement Reid in the late 19th Century. Reid noted a difference in the composition of the faunal remains between the lower and upper regions of these deposits and, therefore, he sub-divided the CF-bF into two main stratigraphic units: the lower Weybourne Crag and the upper Cromer Forest Bed.

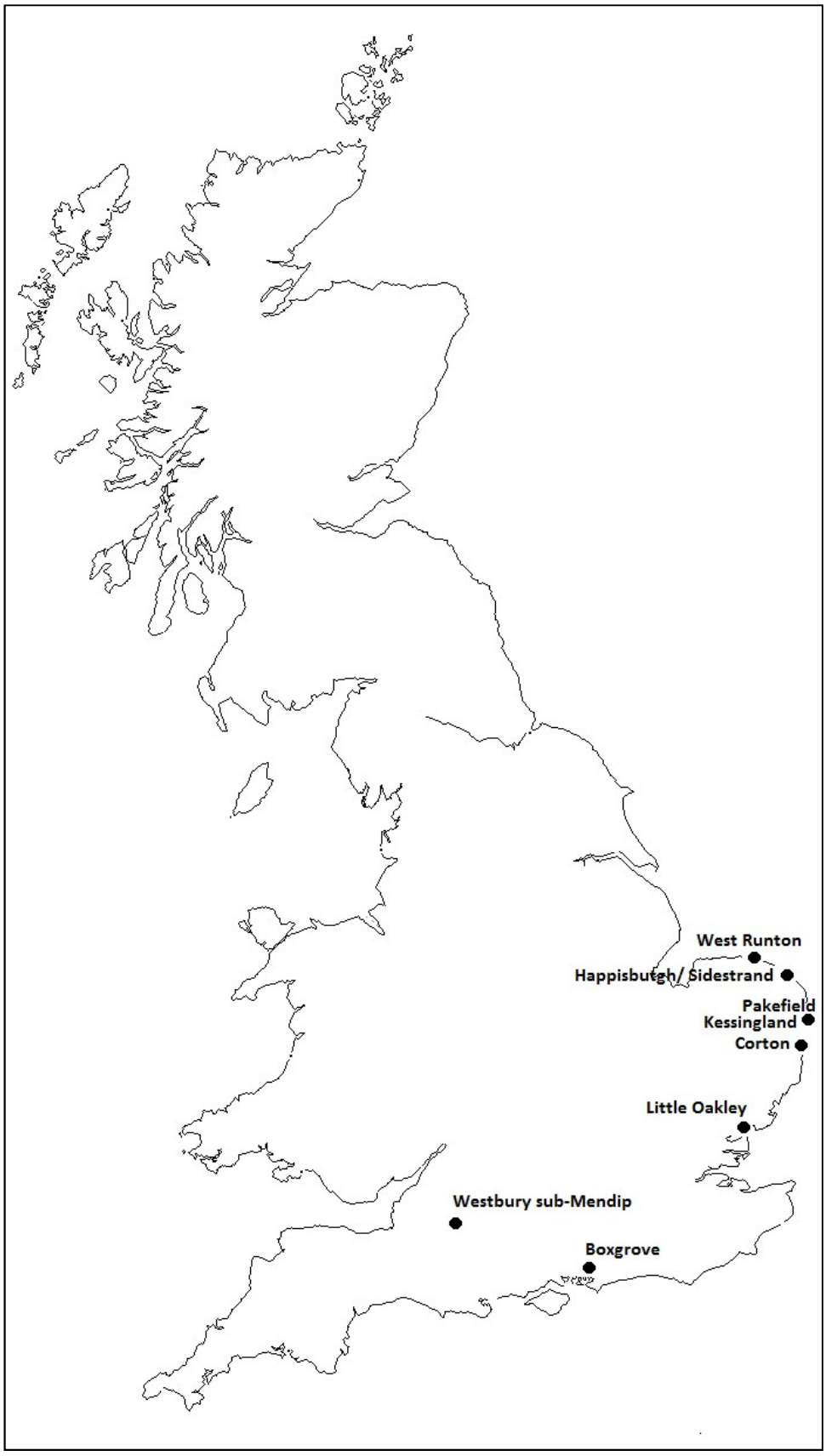

***Figure 1.1**: Location map of the major British early Middle Pleistocene sites discussed in this study.*

The Upper Cromer forest-bed was further sub-divided into the lower and upper freshwater beds, separated by the forest bed (Reid, 1882, 1890). The separation of these two units was based upon differences in the mammalian and floral remains. Reid proposed that the lower and upper Fresh Water beds and the Forest Bed represented the same temperate period, followed by deteriorating climatic conditions (Reid, 1890).

The introduction of more complex analyses, such as the identification of pollen, floral macrofossils and Molluscan remains found within the sediments, has subsequently led to the suggestion that a more complex series of temperate and cool episodes is represented by the CF-bF. On the basis of pollen analysis, West (1980) originally divided the CF-bF into three stages; the Pastonian (temperate, Early Pleistocene), the Beestonian (cold, early Middle Pleistocene) and Cromerian (temperate, early Middle Pleistocene) (Lister, 1998). The Beestonian and Cromerian phases are thought to be separated from the Pastonian sediments by a hiatus comprising a significant period of time, probably over a million years, indicated by significant faunal turnover (Turner, 1996).

There are several biostratigraphically important species within the Cromerian. First, as recognised by Reid (1882) in his 2-stage system, is the difference in age of sites between those containing *Mimomys savinii*, which is recognisable by presence of rooted molars, and those containing *Arvicola terrestis cantiana,* which have continuously growing molars*. A. Terrestis cantaina* is thought to have evolved from its *Mimomys* ancestors prior to interglacial IV of the Cromerian Complex (See Table 1.1 for sub-division of the Cromerian). Throughout Europe, *Arvicola* is always found in deposits above those containing *Mimomys*, and as the presence of unrooted, continuously growing molars provides a clear evolutionary advantage over rooted

molars by extending the functional life of the teeth, this trait is assumed to have spread rapidly throughout populations (Roberts & Van Kolfschoten, 1994).

Other biostratigraphically important species include *Stephanorhinus hundsheimensis (extinct Rhino), Megaloceros verticornis (*Giant Deer) and the large variant of *Mammuthus trogontherii* (Steppe Mammoth). Species such as *Megalocerous savini (*Extinct Giant Deer*)* and *Equus latidens* (an extinct Horse species) are only found in assemblages also containing *Mimomys* and *Palaeoloxodon antiquus (Straight-tusked Elephant)*, *Hippopotamus spp.* while *Stephanorhinus kirchbirgensis (*Merck's rhinoceros*)* is only found in faunas which also contain *Arvicola* and thus assumed to be younger in age (Stuart and Lister, 2001).

More recently, this division of the Cf-Bf into 2 temperate and one cool phase has been suggested to oversimplify the complex series of warm and cold adapted mammalian, molluscan and floral faunas evident (Stuart & Lister, 2001, Preece, 2001). Turner (1996) and Stuart and Lister (2001) point to the evidence presented in oxygen isotope curves of the complex climatic change that occurred during the early Middle Pleistocene (see figure 1.2). This climatic complexity is becoming ever more apparent within the terrestrial record, as evidenced by floral and faunal remains and sedimentology. On the basis of the mammalian faunal evidence, Stuart and Lister (2001) present the biostratigraphic evidence for at least 6 temperate episodes within the Cf-bF in Britain as summarised in table 1.1. Biostratigraphic methods of dating are based upon the assumption that major differences in faunal composition between sites reflect a difference in age.

However, there are several opponents to the Biostratigraphic model who point to the fact there are several contradictions to the division of the Cromerian using

Biostratigraphic methods. Sardella *et al.* (1998), suggest that here are reports of *Arvicola* in much earlier deposits than would be expected if the *Mimomys*/ *Arvicola* rapid evolutionary boundary model is to be believed. However, the dating of these sites has been called into question on the basis of dates gained using Argon isotope dating, which have improved dating ranges compared to the previous Potassium-Argon dating techniques, which suggest the sites are significantly younger than previously suggested (Colorti *et al.*, 2005).

The most frequent argument against the biostratigraphic sub-division of the Cromerian is that based on terrace formation. This argument is based upon the theory that river terrace systems are formed through major river systems forming aggredational terraces during successive periods of erosion, caused by climatic changes linked to c. 100 Kya cyclical orbital forcing (Bridgland, 1994). On the basis of this theory, it is suggested that it is possible to date sediments and sites based on their relative position within a terrace system and in comparison to other systems (Bridgland, 2000).

In the Cromerian, Lee *et al.* (2004) argue against the use of the Mimomys/ Arvicola boundary as a relative dating method in the Cromerian, as they suggest that it is not possible to accurately define first and last-appearance dates of species in sites of this age, and therefore that Arvicola and Mimomys may have existed at the same time. They suggest placing the *Mimomys/ Arvicola* boundary at MIS 17 or 19 rather than the MIS 14 date proposed by the Biostratigraphic model (Table 1.1), on the basis of river terrace correlations. These correlations propose a revised scheme with 6 parallel terraces within the Bytham River. They suggest that many of the warm episodes identified within the Cromerian do not represent discrete interglacial periods, but rather fluctuations within the same interglacial.

However, Westaway (2009) refutes this argument as the two lowest terraces suggested by the Lee *et al.* model project below any deposits of the Ingham River, and concludes that the model proposed by Preece & Parfitt (2000) is supported by the succession of river terraces.

The early Middle Pleistocene is an extremely complex period in terms of the number, timing and nature of the climatic cycles it contains. As a consequence, correlating sites and sediments, both within Britain and in the wider European context, is difficult. . *Microtus* remains are common in many early Middle Pleistocene sites and their rapid evolution and large degree of dental variation makes them ideal candidates to provide information relating to the correlation of early Middle Pleistocene sediments.

Cromer sub-division	Site	Biostratigraphic Groups
Cromer IV	Boxgrove Westbury	7?
Cromer III	Waverly Wood Ostend	6
	Sidestrand/ Trimingham	5
Mimomys/ Arvicola Boundry		
	Little Oakley	4
	Kesslingland/ Pakefield	3
	Sugworth	2
Cromer II	West Runton	1
Bruhnes-Matuyama Boundary		
Cromer 1	Happisburgh 3	

Table 1.1: *Sub-divisions of the Cromerian with relative positions of important sites and their Biostratigraphic grouping, with Cromer sub-divisions based on the Dutch sequence (After Stuart & Lister, 2001).*

Phase	1	2	3	4	?	5/6/7		
Site	West Runton	Sugworth	Pakefield	Little Oakley	Sidestrand	Ostend	Westbury	Boxgrove
Homo spp							•	•
Apodemus sylvaticus	•	•		•			•	•
Apodemus maastrichtensis				•				•
Sicista spp								•
Lemmus spp		•					•	•
Pliomys episcopalism	•	•					•	•
Mimomys savini	•	•	•	•	•			
Arvicola terrestis cantiana						•	•	•
Canis lupus	•		•				•	•
Panthera leo	•		•				•	•
Homotherium latidens	•		•				•	
Crocuta crocuta	•		•	•			•	•
Mammuthus trogontherii	•		•					
Palaeoloxodon antiques			•			•		
Equus ferus	•						•	•
Equus altidens	•		•	•				
Equus sussenbornensis	•							
Stephanorhinus hundsheimensis	•	•	•		•		•	•
Sus suscrofa	•		•	•				•
Hipopotamus spp			•					
Alces latifrons	•							
Capreolus capreolus	•					•		•
Megalocerous dawkinsi			•	•				•
Megalocarous verticornis	•		•	•				•
Megalocerous savini	•		•					
Cervus elaphus	•	•	•	•			•	•
Dama dama	•		•				•	•

Table 1.2: Presence and absence of Biostratigraphically important species throughout the Cromeria Complex (after Stuart and Lister, 2001)

Formation	Member/ site	(Preece & Parfitt, 2002)	Lee *et al*, (2006)
Sheringham Cliffs Formation	Trimingham lake beds	9/11	
	Cromer III	12/ 10	
Lowestoft Formation	Cromer II	12	12
	Lowestoft Till Member	12	12
Happisburgh Formation	Corton Till Member	12	16
	Cromer I		16
CF-bF	Sidestrand Unio Bed	13	19
	Happisburgh 1	13	19
***MIMOMYS/ ARVICOLA* BOUNDARY**			
	West Runton	17	19
	Pakefield	17	19

Table 1.3: Suggested reconstructions of the relative ages and stratigraphic position of British Cromerian sites (Modified from Preece & Parfitt, 2002; Lee *et al*, 2006).

1.2.3 THE RELATIVE AGES OF BOXGROVE AND WESTBURY SUB-MENDIP IN THE CROMERIAN

Of particular interest to this study is the position of Westbury and Boxgrove within the Cromerian Complex.

The age of the Boxgrove deposits at Boxgrove, as part of the Goodwood-Slindon Raised beach, precludes the use of many chronometric dating methods, making dating of the stratigraphic levels within the site extremely complex. The position of the Goodward-Slindon raised beach, the uppermost formation of the West Sussex Coastal Plain sequence, demonstrates that the site is older than those found within the lower terrace formations, its proposed age being ca 500,000 years,. The sediments at Boxgrove show a temperate fauna at the base of the sequence, with climatic deterioration towards the top of the sequence to cold, open conditions (Roberts, 1999b).

Several chronometric dating methods have been applied to material from the Boxgrove site: thermoluminescence, electron spin resonance and uranium series, which provided dates of 175.3-319.9, 205-281 and >350 Kya BP respectively (Parks & Rendall, 1999; Grùn, 1999; Rae, 1999). These dates clearly differ hugely, and place the site within a range from MIS 6-11, with no clear consensus between methods. In an attempt to rectify these conflicting dates, Amino Acid Racemization was attempted on molluscan remains (Bowen & Sykes, 1999) the results suggesting dates of 423-362 Kya BP (within MIS 11). Biostratigraphic correlations based on nanoplankton suggested an age of 423-326 Kya, again correlating with MIS 11, whereas the mammalian biostratigraphy correlates with MIS 13 (523-478 Kya BP) (Roberts & Parfitt, 1999).

Clearly there is a great deal of disagreement between the results gained from the various dating techniques. But on the basis of these studies, the most parsimonious date for Boxgrove is either MIS 11 or 13.

The best lines of evidence for dating Boxgrove is mammalian biostratigraphy, as the two interglacials either side of the Anglian Glaciation (i.e. MIS 11 and 13) have distinctive faunal suites (See table 1.1). The presence at Boxgrove of *Arvicola terrestis cantiana*, which is easily recognisable by its continuously rooted molars, is particularly important, as the earliest known examples of this species come from Cromerian interglacial III, with earlier sediments containing *Mimomys savinii*, which has rooted teeth. This would suggest that the site must belong at or after Cromerian III.

Species such as *Ursus deningeri* (Deniger's bear), *Pliomys episcopalis* (extinct forest vole) and *Stephanorhinus hundsheimensis* (extinct rhinoceros) are also present at Boxgrove. These species are known to have become extinct in the UK during the Anglian glaciation and therefore point towards a pre-MIS 11 date for the Boxgrove sediments (Parfitt, 1999).

Establishing the age of the Westbury sediments is also a complex challenge. ESR dating of mammalian remains from the site suggested that the eastern and western stratigraphic sequences were of significantly different ages (for explanation of the stratigraphic sequence at Westbury, see chapter 2). This is at odds with the observed stratigraphy, which suggests that the units are equivalent in age (Grn & Stringer, 1999).

The mammalian remains at the site provide the largest sample and most reliable method of dating the site. Dating of the basal Siliceous Member sediments using biostratigraphical methods is difficult as the mammalian remains are derived and may

not all be of the same age. However, the mammal species which are present; such as *Leptobos,* suggest an Early Pleistocene age (Gentry, 1999). Further descriptions of the stratigraphic sequences at Boxgrove and Westbury can be found in chapter 2.

Fauna of the Calcareous Member (located above the Silicious Member) suggests an early Middle Pleistocene date. The presence of *Arvicola* at the site suggests that Westbury is likely to post-date the Early Middle Pleistocene site at West Runton, where *Mimomys savini* is present. Other species such as *Hemitragus bonali* (extinct Bison), *Cervus elaphus* (Red Deer) and *Panthera leo* (Lion) suggest that the Calcareous Member is best correlated with the Early Middle Pleistocene, as part of the Cromerian Complex (Currant, 1999). *C. elaphus* P_3 remains from the site exhibit a morphology which is similar to that found at West Runton and Clacton and is less advanced than those found at the MIS 9 site at Grays Thurrock (Schreve, 1997; Gentry, 1999). The carnivore fauna at Westbury also shows a mixture of Villafranchian (Early Pleistocene) and Galarian (upper Lower Pleistocene/ Middle Pleistocene) faunas (Turner, 1999). Placing an exact date on the sediments is further hampered by the successive warm and cold periods, as discussed above.

Two temperate periods separated by a cooler period have been shown at Westbury and two possibilities exist; - that the two temperate periods at Westbury are attributable to two separate interglacial periods within the Cromerian Complex, or that they represent a fluctuation in temperatures within a single interglacial period (Andrews & Stringer, 1999). The cool phase represented within the stratigraphic sequence contains several species that require unfrozen ground, suggesting that the temperatures never reached fully glacial conditions. In addition, the minimal variation in the faunal composition of the temperate stages, despite a cooler phase in-between,

led Schreve *et al.* (1999) to suggest that the most likely scenario is a fluctuation in temperatures within a single interglacial period, most likely the Cromerian Interglacial IV. Andrews (1990) also suggests that the evidence points to an interglacial period with two peak interglacial fluctuations.

The Calcareous Member remains at Westbury appear to have strong correlations with those found at Boxgrove, based upon these biostratigraphic similarities and the dating evidence described above. Andrews (1999) considers the fauna at Boxgrove and Westbury to belong to the same period. However, Parfitt and Preece (2000) refuted this, on the basis that *M. gregalis* is found at Boxgrove, whereas Westbury has only *P. gregaloides*, which they considered to be the ancestral form. On this basis, Boxgrove must be younger than Westbury.

1.2.4 CORRELATIONS OF THE BRITISH LOWER MIDDLE PLEISTOCENE WITH EUROPE

Correlations have been drawn between the stratigraphy of the Cf-bF and deposits believed to be of a similar 'Cromerian' age in other regions of Europe, particularly those in the Netherlands and Germany. These correlations are based largely upon the mammalian and molluscan biostratigraphic evidence, but, owing to the complexities of both the British and Continental records finding direct correlations between sites believed to be of similar age is difficult (Zagwijn, 1996).

Correlations between British and European sites of a similar age have been proposed on the basis of biostratigraphical correlation. The Cf-bF is thought to correlate with the Cromerian Complex found in the Netherlands, which comprises four distinct temperate

phases (Cromer I, II, III and IV), and has also been found to correlate with several German sites, such as Miesenheim and Karlich. (Zagwijn, 1996, Stuart & Lister, 2001).

However, the difficulties in correlating sites that are geographically distant, combined with the fragmentary nature of the available sediments and biological remains, (particularly within the Dutch sequences) means that, at this stage, all correlations are tentative. Proposed correlations between Dutch, German and British sequences can be seen in table 1.4

	Netherlands	Germany		England	
		Parfitt & Preece (2002)	Zagwijin (1996)	Stuart & Lister (2001)	
Cromer IV	Noordbergum	Miesenheim	Bilschausen/ Karlich	Boxgrove Westbury Waverly Wood	5/6/7?
Cromer III	Rosmalen	Karlich G		Ostend Sidestrand/ Trimingham	
Mimomys/ Arvicola					
Cromer II	Westerhoven	Karlich F Karlich C	Hunteburg	Little Oakley Kessingland/ Pakefield Sugworth West Runton	4 3 2 1
Bruhnes/ Matuyama					
Cromer I	Waardenburg	Karlich B	Osterholtz		

Table 1.4: *Alternative correlations of British and European sites of Cromerian ages (Modified from Stuart & Lister, 2001; Parfitt & Preece, 2002; Zagwijin, 1996).*

1.3 THE BIOLOGY AND BEHAVIOUR OF *MICROTUS* SPECIES

1.3.1 INTRODUCTION

The genus *Microtus* represents an extremely diverse, rapidly evolving, group of small mammals. Owing to their widespread nature and important role in many ecosystems, the biology and behaviour of *Microtus* species is well studied. In order to interpret the archaeological data presented within this study, a full understanding of the biology and environmental responses of *Microtus* species is required. This section introduces the genetic relationships between species of *Microtus* and the effect of genetic and environmental factors upon *Microtus*, which is essential when trying to interpret morphological variation in the M_1.

1.3.2 COMPLEX GENETIC HISTORIES.

Microtus is one of the most speciose mammalian genera throughout the Holarctic (a zoogeographic region that extends from the North Pole to 30-45° latitude), with over 60 species having been identified. *Microtus* species are ecologically diverse, although most species prefer open grasslands (Nowak, 1999). In many archaeological assemblages, *Microtus* species are the dominant herbivorous small mammal (Andrews, 1990).

The evolutionary and genetic relationships of extant species of *Microtus* have been well-studied in recent years. *Microtus* species have a large amount of intra-specific variability, adaptive convergence and frequent instances of sibling-species, all identifiable by morphological characteristics (Zakrzewski, 1985; Chaline & Graf, 1988; Nadachowski and Zagorodnyuk, 1996; Chaline *et al*., 1999). However, *Microtus* species have also been shown to display a much larger amount of karyotypic variation than

most mammalian species (Maryama & Imai, 1981), which is not always reflected by obvious morphological characteristics (Baskevich, 1996). This leads to no apparent phylogenetic trends to the karyotypic variation (number or appearance of chromosomes) among closely related species (Chaline *et al*., 1999; Machola *et al*., 2001). Recent DNA studies have shown that the genus *Microtus* contains many closely related sub-species. Within these sub-species, there is an extensive amount of intra-specific variation which provides clear evidence that the recognised species are not static forms but are clearly continuously differentiating. It is suggested that the radiation of *Microtus* from their *Allophaiomys* ancestors occurred approximately 2 Mya. This radiation resulted in seven major sub-genera: *Microtus*, *Agricola/Neodon*, *Terricola*, *Stenocranius*, Nearctic species (including *Agricola*), *Stenocranius* and the *Pallasiinus/ Volemys/ Alexandromys* grouping (Jaarola *et al.*, 2004). Detailed relationships between and within species are shown in figure 1.2.

Of the 4 species of *Microtus* included in this study, two species, *M. arvalis* and *M. agrestis,* have been studied in detail with regard to their phylogeographic variation. Both species display a high degree of phylogenetic variation, as has been demonstrated for other *Microtus* species (e.g., Van de Zande *et al.*, 2000; Conroy *et al.*, 2001; Conroy & Cook, 2000; Martĭnková *et al.,* 2007). Therefore, although no published data exist on *M. subterraneus* and *M. gregalis,* there is no reason to think they will not also display a high degree of phylogenetic differentiation, in line with all other *Microtus* species. In *M. arvalis*, 5 genetic lineages have been indentified, falling into clear geographic boundaries: Eastern, Italian, Western, Central, and a clade that corresponds to the karyotypically distinct 'obscurus' lineage, which is found in Russia, Romania, Armenia and Siberia (Haynes *et al.*, 2003; Tougard *et al.*, 2008; Uhlikova, 2004).

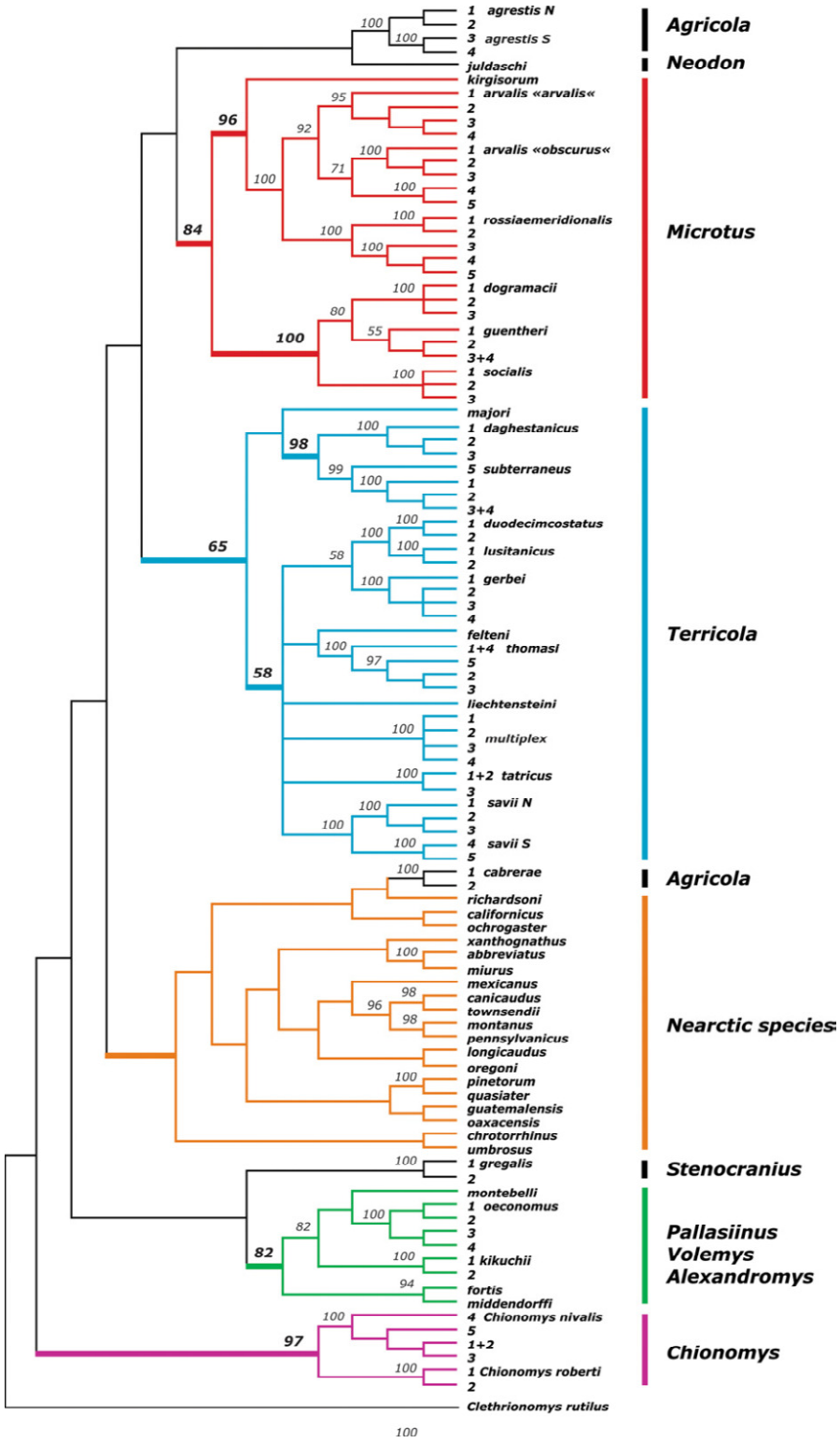

Figure 1.2: *DNA reconstruction of relationships between Microtus species (Jaarola et al., 2001).*

M. agrestis also displays clear genetic differences within geographic regions, with groupings in Eastern, Western and Central Europe (Jaarola & Searle, 2004; Jaarola and

Searle, 2002). For both *M. arvalis* and *M. agrestis*, these distinct lineages are thought to have evolved after the Last Glacial Maximum (LGM) circa 23000 years ago. The glaciation of much of Europe is thought to have pushed species into 'refugia' of suitable habitats (eg; Stewart & Lister, 2001; Sommer & Nadachowski, 2006; Provan & Bennett, 2008). Once the ice receded, these populations are thought to have re-populated Europe. Due to the genetic bottle-neck effect this would have caused, the genetic relationships within species prior to this event are not well understood. However, GMM analysis of modern specimens may provide information as to whether phylogeographic genetic differences can be observed within the dentition of *Microtus* species.

1.3.3 SEXUAL DIMORPHISM.

Sexual dimorphism includes any systematic difference between mature male and female individuals of the same species. This difference may take several forms, including colour, the presence or absence of elements used in courtship rituals or for the specific purpose of attracting a mate (e.g. antlers in male deer or the tail feathers in a male peacock), or a difference in size between males and females. Difference in size has been explained as being caused by more active competition between males for a mate than in females, with females being more attracted to males which are perceived to have the strongest genes (i.e.; robust, healthy males) (Lindenfors *et al.*, 2007). Sexual dimorphism may also be caused by ecological factors; body size differences may arise so that sexes can utilise difference resources within an ecological niche and not compete for the same resources (Shine, 1989).

Sexual dimorphism has been shown to be present in many *Microtus* species, and has been measured both as an increase in overall length of living specimens, or in body

mass in male specimens in comparison to female specimens (Heske and Ostfeld, 1999, Boonstra *et al.*, 1993, Gromov and Polyakov, 1999). The degree of sexual dimorphism present within a species of *Microtus* has been suggested to be influenced by the mating system of that particular species, with polygnous species displaying greater size difference between species than promiscuous species, which in turn would display more dimorphism in size between species than monogamous species due to the role of competition between males (Boonstra *et al.*, 1993).

Within the archaeological record, the identification of sexual dimorphism within a dataset may be much more difficult to achieve, due to the lack of articulated skeletons and high likelihood of taphonomic damage to many skeletal elements (Andrews, 1990). This study focuses on the lower M_1 of several *Microtus* species, as this is the skeletal element which is most commonly preserved intact within archaeological deposits. It could be hypothesised that a larger, more robust (male) specimen would have a larger cranium, and therefore larger teeth. However, other than in a few specific species such as humans, where there is a general increase in tooth size in males compared to females (Brace & Ryan, 1980), or where increased tooth size, particularly in canines is used as part of sexual display, such as in chimpanzees (Leutenegger & Kelly, 1977), sexual dimorphism is rarely reflected within the dentition of mammals (Hillson, 2005). Therefore, it is important to initially investigate evidence of sexual dimorphism in *Microtus*, reflected in the size and shape of M_1 teeth in the species included within this study to avoid bias.

1.3.4 VARIATION IN SIZE AND SHAPE.

Allometry

Allometry is the relationship between size and shape of an organism or skeletal element, as first outlined by Snell (1892) and Huxley (1932). Within the study of biological organisms, there are two main focuses of allometric study: firstly, in the study of ontogenetic change- how the shape of an organism or skeletal element changes as an individual grows and matures, where the relative proportions of skeletal elements may change with size as an individual grows (allometric scaling) or the relative proportions may remain the same (isometry)(e.g. O'Higgins and Jones (1998); Ponce de León and Zollikofer (2001); Cobb and O'Higgins (2004).

Allometry in biological organisms may take many forms that have been investigated using GMM methods such as ontogentic allometry- variation of size that is due to growth of an individual until it reaches maturity (e.g. O'Higgins and Jones 1998; Ponce de León and Zollikofer 2001; Cobb and O'Higgins 2004). GMM methods have also been used to investigate evolutionary allometry, i.e. differentiation in size and shape between different evolutionary lineages (e.g. Klingenberg 1996; Milne and O'Higgins 2002).

However, as only fully adult *Microtus* teeth are included in this study, the second focus of allometric studies is of greater interest; the relationship between size and shape of skeletal elements in individuals of the same age (static allometry). In most multivariate statistical methods used in Geometric Morphometrics, size is removed from the study of shape using Generalised Procrustes Analysis. However, if there is a large allometric component within a dataset, this may still have an effect upon the results gained from the analyses. In samples where a large amount of allometry is

present, it can result in the first principal component consisting entirely of shape variation caused by size, which would be desirable to remove (e.g. Penin *et al*., 2002; Frost *et al*., 2003; Mitteroecker *et al*., 2004).

Environmental change

The specific issue of the effect of climatic fluctuation on the size of the dentition of a *Microtus* species, *Microtus (terricola) grafi* has been assessed by Mointure and Brunet-Lecomte (2004). They found that no direct correlation between tooth size and either climate change or body size is suggested. In contrast, they did find that some morphological variation can be attributed to climatic change, with the pitymyn rhombus becoming less tilted in warm conditions than those in colder conditions.

The effect of long-term climatic change upon rodent morphological evolution has been investigated by several authors who have hypothesised that significant changes in ecological opportunities caused by climatic change may be responsible for morphological change of rodent teeth (e.g., Renaud et al, 2005, van der Meulen & Daams, 1992). The change in ecological opportunities is due to the opening of environments which allow evolution of specialist species such as *Stephanomys*, whereas more generalist species with wider habitat and climate tolerance ranges are less likely to change through time. However, analyses of another Arvicoline species (in the same sub-family as *Microtus*), *Arvicola cantiana*, suggests that that species shows great variability but with no easily discernable trends or patterns in M_1 morphology through time (Escudé et al, 2008).

Environmental factors

Variability in the size and shape of mammalian species has been of interest to scientists for many years. Variation in body size has generally been linked to the ecological niche of the species (eg Maurer et al, 1992) whereas morphological variability has been associated with several different factors such as ecological distribution, systematics and biochronology (Thorpe, 1987, Brunet-Lecomte, 1991, Maul et al, 1998). Literature concerning the effect of environmental and temporal factors upon the morphology of *Microtus* M_1 teeth is limited, as analyses of palaeontological remains have tended to look towards the presence or absence of species as a biostratigraphic tool, or to aid climatic and habitat reconstruction via correlations with the climatic and habitat tolerances of modern species (Eg; Currant & Jacobi, 2001., Schreve, 2001, Cordy, 1999). Attempts have been made to understand the effects of several factors on the dental morphology of rodents. Renaud (1999) investigated the effect of environmental conditions upon the dental morphology of a West African rodent *Oenomys*. Climatic conditions have also been shown to have an effect (Eg; van Der Meulen & Daams, 1992; McGuire, 1999). Temporal change through time in dental morphology has also been investigated in *Microtus* species (Nadachowski, 1984). However, these changes have been complex and difficult to interpret easily due to the presence of other factors that may have affected the morphology, such as genetic change.

The size of mammalian teeth can vary for several reasons, as noted in chapter 4 (section 4.2). The specific issue of the effect of climatic fluctuation on the size of the dentition of a *Microtus* species, *Microtus (terricola) grafi* has been assessed by Mointure and Brunet-Lecomte (2004). They found that no direct correlation between

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1.3.5 DISPERSAL RATES AND MODES

In common with many small mammal species, and in particular, rodents, most populations of *Microtus* species display a 'boom and bust' population cycle. That is to say that population numbers may fluctuate periodically within a certain area as population size places pressure upon individuals within a population to disperse into new areas.

Several competing theories have been proposed as an explanation for this fluctuating population density and the modes of dispersal within *Microtus* species:

Greenwood (1980) and Dobson (1982) suggest that dispersal in *Microtus* species is an evolutionary trait designed to reduce the amount of in-breeding within populations. Therefore, as populations grow, and the numbers of offspring increase within a population, juveniles disperse, leading to the peak population comprising mainly adult individuals. Competition for resources has been suggested as a possible dispersal cause (Moore and Ali, 1984; Putsey, 1987).However, the freedom of individuals within a low-density population to move across large areas free from competition, which are then restricted as population size grows and pressure from neighbours decreases, has also been suggested. An alternative explanation has also been suggested by Krebs *et al.,* (1973) in which density-intolerant individuals disperse during the population increase phase, leading to the majority of individuals remaining within a population being density-tolerant. These individuals are also seen to be the most aggressive, which leads to decreased reproductive success and survival rates. Once population densities decrease again, density-intolerant individuals may migrate into the population, causing population increase again.

1.3.6 DENTAL MORPHOLOGY

Microtus dentition is hypsodontic or continuously growing. This trait appears to have evolved approximately 2Mya within the *Allophaiomys* ancestors of *Microtus* (Repenning *et al.*, 1990). It has been proposed that evolution of hypsodont molars, combined with coronal cementum (cementum located over the enamel in the crown) and prismatic enamel occlusal patterns, developed due to selective advantage in species shifting from feeding on seeds and fruits to tough plant material, such as silica-rich grasses (Romer, 1966). The presence of continuously growing teeth will dramatically extend the life-span of the teeth, and therefore of the individual, meaning that there will be a strong selective pressure on individuals with hypsodontic molars, and the trait would be expected to spread rapidly through the population.

Analysis of the rate and processes of tooth formation within Microtine rodents has shown that it can be divided into four distinct ontogenetic phases; the occlusal surface of the tooth is the first ontogentic phase of tooth formation, then the side-walls of the crown are formed, followed by the formation of the crown-base and finally the formation of roots. In *Microtus* species, with their hypsodontdic teeth. It appears that the second stage, the formation of the side-walls of the crown, is extended throughout the life of the animal, so the crown and roots of the teeth are never formed (Von Koeningswald & Van Kolfschoten, 1996).

It has been suggested that Microtine rodents have achieved a considerably greater amount of evolution in the Pleistocene (c. 2.3 million years) than most other species have over the entire Cenozoic Era (c. 63 millions years) (Bader, 1965). This rapid evolution and speciation has been reflected in the dentition of *Microtus* species. It has

been demonstrated that the anterior portion of the M_1 and posterior portion of the M^3 are the dental characters most affected by phylogenetic change are also those which vary the most between and within populations (Gutherie, 1964). The generalised structure and naming conventions of *Microtus* teeth can be seen in figure 1.3.

Microtus teeth are extremely variable not only between populations and species but also within species and populations. For example, Kapischke *et al.* (2009) have identified 7 distinct morphologies in the M_1 of *Microtus agrestis* specimens from Germany. These morphotypes illustrate a high degree of morphological variability, mainly concentrated around the AC region of the tooth (Fig 1.3). The most common form of variation observed by the authors is the division of the AC region into several closed loops. T6 or T7 may become separated from the rest of the AC region by a narrowing of the enamel between BRA4 and LRA5 (as in examples E, F and G in figure 1.4), or the anteroconid complex may become separated entirely (example C). Examples A and B also illustrate the differences that may be seen in the relative positions of the different components of the AC region. The examples shown within this figure are relatively extreme examples of the variation which is likely to be found in a species; however it illustrates the plasticity and large degree of variance which may be found in the shape of the M_1 in *Microtus* species.

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Figure 1.3: *Descriptive definitions of regions of Microtus teeth. (Adapted from Van der Meulen, 1976)(T= triangle, B= Buccal, L= Lingual, SA= Salient angle, RA= Re-entrant angle, PL= posterior loop, AL= anterior loop, AC= anteroconid complex)*

Figure 1.4 *Different morphologies of M. agrestis M1 teeth within Germany, (Modified from Kapischke et al., 2009) The AC region of the tooth is outlined in green. (A= standard Morphology, B= pronounced curve on lingual edge of AC region. C, D and E= constriction of AC region to various degrees causing sub-division. F and G= Anterior loop separated by increased indentation of area between T6 and T7).*

These observations, combined with the findings of Gutherie (1965) discussed above, suggest that the AC region of the tooth is likely to be the most informative in terms of relationships within and between species when analysed using GMM methods. This may prove to be problematic, as in ancient material the AC region is also the region of the tooth which is most commonly damaged due to taphonomic factors (Andrews, 1990).

Food specialisation has been shown to affect the structural parameters of dental patterns in Arvicoline rodents, with species feeding on roots having a less complex pattern and number of triangles in their teeth, but a larger percentage of enamel on the tooth surface than those species which feed on leaves or which have a mixed diet. This difference in enamel structure has been attributed to the need for thin, sharp enamel edges to cut tough, siliceous material, such as leaves. In contrast, thick, blunt enamel is required in order to crush tough, dense material such as seeds or material contaminated by soil, such as roots (Herrmann, 2002).

Studies have also shown that in Arvicoline species with continuously–growing molars, the AC region significantly changes shape from juvenile to adult (Figure 1.5). The size of the AC region increases significantly over time and becomes more complex in shape. This difference is not a result of ontogenetic change, but rather is an artefact of the amount of wear the dental tissues have been subjected to. In juvenile individuals, the AC region of the tooth contains many folds and protrusions, rather than the standard smooth curve seen in fully adult individuals. Once individuals are fully adult, their tooth morphology remains the same, and the overall morphology of the tooth is unaffected by wear (Viriot, 1996).This suggests that only fully adult individuals should be considered within this study.

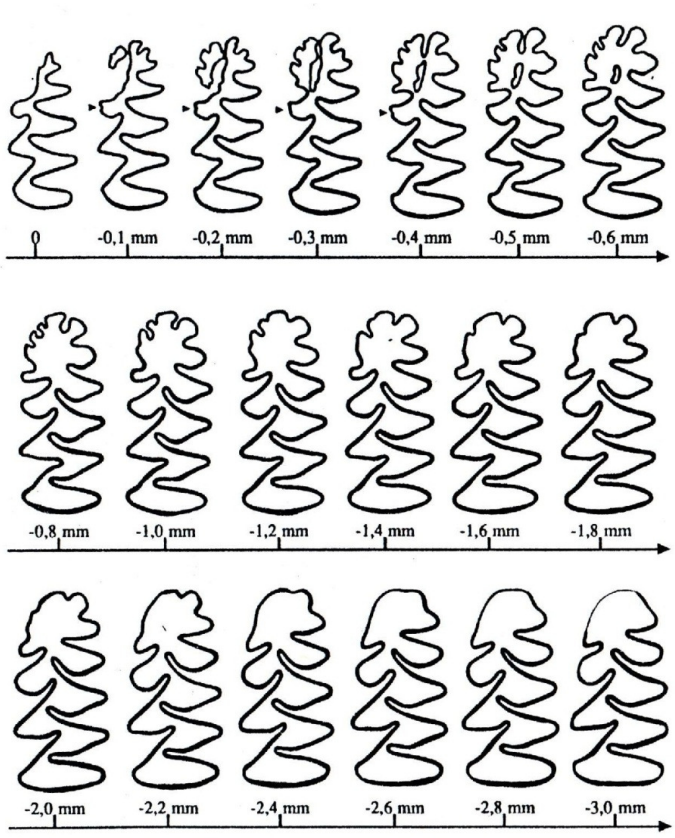

Figure 1.5: *Schematic diagram of the varying morphology of Microtus teeth according to wear (adapted from Viriot, 1996).*

1.4 APPLICATIONS OF GEOMETRIC MORPHOMETRIC ANALYSES

This section aims to introduce the applications of Geometric Morphometric methods to biological material and introduce the background to previous research which has helped to form the hypotheses and questions in this study.

1.4.1 INTRODUCTION TO GEOMETRIC MORPHOMETRIC ANALYSES

The application of GMM methods to archaeological material is a relatively new development, and, as such a clear understanding of the applications of GMM methods is required. This section aims to introduce some of the research questions to which GMM analyses have successfully been applied and to provide background information

and justification for the selection of GMM methods for analysis of the material within this study.

Morphometric measurements of skeletal and soft-tissue elements are a standard component of biological and palaeontological analyses. These are usually linear measurements (eg; the greatest length or breadth of a biological element). Qualitative assessment of shape also traditionally plays a large role in the description and explanation of morphological components. Both of these approaches have their drawbacks. Firstly, linear measurements of skeletal components are independent of one another and, therefore, gaining an insight into how the change in one measurement affects another is difficult. Even in the most comprehensive study, linear measurements also mean that large proportions of the organism or element being studied are not described, and linear measurements by definition are measuring size rather than change in shape. Qualitative descriptions of shape are unreliable descriptors of shape as they are subjective and open to interpretation (Bookstein, 1991).

The field of Geometric Morphometrics has grown up in an attempt to address issues with traditional methods of quantifying biological elements such as linear measurements or qualitative descriptions of shape. Geometric Morphometrics provides methods which allow both a comprehensive analysis of biological shape mathematically and the ability to represent these results graphically so that shape variation can be seen visually. The development of these methods has primarily occurred over the last 20 years or so by Bookstein (1986, 1991), Kendall (1984), Rohlf (1990, 1996) Goodall (1991, Goodall and Bose, 1987), O'Higgins (1997), Klingenberg (1996) and others.

Due to the advantages represented by the use of GMM over standard morphometric methods, the techniques used have become an important part of the analysis of biological remains.

One of the major applications of GMM methods has been the identification, quantification and description of morphological variation between and within populations and species. One of the most important questions within biological contexts is to find criteria that allow groups to be reliably distinguished, and usually the criterion is in the form of the shape of a biological structure (Sneath & Snell, 1973). Standard methodologies used to describe biological organisms or structures are usually based upon linear measurements (for examples see Von den Driesch, 1978) or qualitative descriptions. GMM methods circumvent the problematic issues related to standard measurement schemes by allowing the shape of an organism or element to be captured in much greater detail and for the effect of changes in shape upon the element as a whole to be easily examined and visualised.

1.4.2 GEOMETRIC MORPHOMETRICS AND SYSTEMATICS.

There are three different kinds of systematic questions for which GMM methods can be used. Firstly, there are taxonomic questions that aim to identify and provide criteria for discrimination of species, which may appear morphologically similar or make up a 'population'. Secondly in the theoretical reconstruction of phylogenetic relationships between taxa. Thirdly, systematists are concerned with the evolutionary history of biological features (Zelditch *et al*., 2004).

GMM has been proven to be a highly effective suite of methods to discriminate between closely-related species, even in the case of sub-species that are differentiated on the basis of karyotypic difference (e.g. in shrews: Polly 2003).

The use of morphological characteristics and measurements in systematic biology is a standard approach used by biologists and taxonomists. In ancient material in particular, the use of morphological characteristics to identify species and to infer links between extant and extinct species is an invaluable tool and often the only source of information available for such reconstructions. However, as DNA analyses have become more widespread, the role of morphometric analyses in identifying systematic relationships amongst living or more recent taxa has diminished.

The rise of Geometric Morphometrics and the advantages of this method over standard metric techniques, as described above, leads to the possibility of more in-depth analysis of the relationships between species. However, the use of morphological differences or change to infer phylogenetic relationships is a far more controversial subject.

Zelditch *et al.*, in the mid- 1990s, published a series of papers in which they used partial warp scores (a method of mathematically quantifying the variation in shape from the mean shape of the dataset) as characters upon which to base phylogenetic reconstructions (Fink & Zelditch, 1995; Zelditch *et al.*, 1995; Zelditch *et al.,* 2000). However Rohlf (1998) and others consider this method, in particular, to be inappropriate for use in systematics as partial warps are not homologous and biologically meaningful variables, and deformation patterns are not determined by patterns of co-variance within the dataset. Relative warps of individual regions of landmarks in a complex configuration have also been suggested as a more accurate

method for the construction of phylogenetic relationships and reconstructing phylogenies (Macleod, 2002).

The reliability of the methods has been widely debated and as a consequence they are not commonly used. However, alternative methods of using GMM data to estimate phylogenetic relationships by constructing trees has been widely used in the last decade or so (for examples see Camul & Polly, 2005; Moraes *et al.*, 2001; Cardini & O'Higgins, 2004, Klingenberg & Ekau, 1996). Many of these studies have shied away from using trees as a method of reconstructing phylogenies. However, many other studies have found a significant correlation between morphology and phylogeny in some closely related species (Cardini, 2003; Polly, 2003). Caumul and Polly (2005) have suggested that molar shape in rodents is a reliable feature in phylogenetic reconstructions. This is due to their relatively slow evolution and the low amount of ecophenotypic morphological variation, leading to a stronger phylogenetic signal than carried by other skeletal elements, such as skulls or mandibles. They also discovered that, although the relative contribution of mtDNA to molar morphology in Marmots was significantly smaller than that of factors such as diet and body size (5%, 9% and 15% respectively), a strong and reliable phylogenetic signal was recoverable in molar morphology. Polly (2001) has also shown that in *Sorex araneus*, GMM methods can be successfully used to distinguish between very closely linked species which are indistinguishable by eye and are separated by karyotypic differences, and produce reliable trees based upon GMM data which reflect phylogenetic relationships. For examples of tree-estimation methods used in this study, see 3.5.8.

Microtus species, due to the high amount of variability between populations, rapid diversification and high degree of speciation (Gutherie, 1965), may be expected to be

an excellent candidates for the reconstruction of phylogenetic relationships through GMM analyses of dental morphology.

1.4.3. THE APPLICATION OF GEOMETRIC MORPHOMETRIC METHODS IN ARCHAEOLOGICAL CONTEXTS.

The application of GMM methods to answer archaeological questions is a relatively new development, compared with its use in Biology and Palaeontology. In archaeological contexts, the questions GMM methods are attempting to answer usually involve the use of mammalian species as a proxy rather than specifically investigating the taxonomy or morphology of a particular species in the context of other similar species.

Several interesting studies have used GMM methods to investigate morphological change in the dentition of rodent species to explore the potential of using changes in tooth morphology as a climatic indicator. Renaud (1999) has shown there is a significant climate related size-difference in the East African rodent *Oenomys*. Of most interest to this study is the finding that GMM methods can be used to identify subtle morphological changes in the M_1 of *Microtus californicus,* which are highly correlated with climate (McGuire, 2009).

GMM methods have also played a part in the identification of new species. For example, Cucchi *et al.* (2006) identified a significantly different morphology in the dentition of the house mouse*, Mus musculus,* on the island of Cyprus. Specimens from the island were confirmed to be a separate species on the basis of DNA analysis.

Another branch of Archaeology in which the potential of GMM has recently been applied is exploring the migration and movements of humans through the movements

of mammalian species that humans intentionally or unintentionally took with them. Cucchi *et al.* (2002) have shown that it is possible to identify different species of *Sus* in Island South East Asia, suggesting possible trading and migration between island communities.

A similar methodology has also been used in an attempt to understand the movements of people around the Mediterranean by investigating the origin and links between house mouse populations using GMM analyses of their dentition (Cucchi *et al.*, 2004, 2005; Michaux *et a.l*, 2007). The migration of humans and origin of human remains have also been analysed using GMM methods (Eg; Neves *et al.*, 2005), and GMM methods have been used to model variation in lithic technology through time.

1.4.4 DISCUSSION

Geometric Morphometric methods are able to provide detailed information regarding shape variability and variation. In the case of the *Microtus* species selected for analysis within this study, a great deal of research into the variability in shape of the M_1 and other cheek-teeth has been undertaken in the last 100 years or so. One draw-back of such research, however, is that the majority of criteria used, in terms of identification of species or variability in shape between species, have been descriptive. Such qualitative criteria can be extremely subjective from one researcher to another and, due to the high degree of inter- and intra-population variability in dental morphology observed in *Microtus* species, may also be extremely variable depending on the source material.

Geometric Morphometric forms of analysis have been chosen as the primary method of data collection for this study, for several reasons.

- GMM methods allow the amount of variability within and between populations of *Microtus* to be quantitatively measured.
- Morphological changes in the shape of the M_1 are easily visualised, and the regions of the tooth in which variation occurs can be easily identified.
- GMM methods allow the shape of the M_1 to be analysed independently of shape, in comparison with standard linear measurements where standard measurements are based upon greatest length/ breadth of particular regions of the tooth, and, therefore, are inherently based upon size.
- GMM methods have been shown, in other species, to successfully identify and separate closely related species with similar morphological characteristics and to reconstruct phylogenetic relationships between species with a high degree of accuracy.

As can be seen from the information in section 1.2.2, the Lower Middle Pleistocene in the UK is represented by series of complex sites for which correlations are not always clear. The rapid evolution of *Microtus* species, combined with their high inter and intra-specific variability and frequent recovery from sediments of this age, makes them ideal candidates for an in-depth exploration into correlations between sites. GMM methods represent a clear advantage over standard quantitative methods used in Palaeontology, and may allow relationships between and within species to be quantified and analysed accurately.

The information provided within this chapter has served as an introduction to the context and sub-division of the Lower Middle Pleistocene in Western Europe, the biology and behaviour of *Microtus* species and the current used and context of Geometric Morphometric techniques. Chapters 2, 3 and 4 will provide more in-depth

information on the specific sites investigated in this study, the taxonomy of *Microtus*, and the methods of analysis.

1.5 OVERVIEW OF THESIS

As discussed (section 1.1), this thesis aims to evaluate the use of GMM methods to identify and investigate morphological variability within and between *Microtus* species and to understand the relationships between dental morphology and evolutionary and environmental processes.

Firstly, the archaeological sites from which samples were taken are presented in detail (chapter 2), followed by an in-depth introduction of the taxonomy, ecology, identification criteria and morphology of the *Microtus* species included in this study (Chapter 3). Chapter 4 explains the principles of Geometric Morphometrics and explains the statistical tests which are used throughout the study.

A modern dataset is tested, in order to refine the GMM methodology and to gain an in-depth understanding of the ability of GMM methods to identify inter- and intra-species variation using morphological characteristics of the M_1 (Chapter 5).

The findings from chapter 5 are then applied in chapter 6 to a well-dated, well stratified Late Pleistocene site from Belgium, Walou cave, to investigate further the role of environmental and evolutionary changes on Microtine dental morphology.

Chapters 7 and 8 apply the established methodology to two early Middle Pleistocene sites from the UK, Boxgrove and Westbury sub-Mendip to investigate the central aim of the thesis- to increase understanding of the stratigraphic sequences and climatic variation at those sites, at a site-specific level. Chapter 9 then moves on to look at how the data gained from this study may influence our understanding of the relative ages

of Westbury and Boxgrove and the impact upon our understanding of these sites in the UK early Middle Pleistocene and their wider European context.

CHAPTER 2
SITES AND STRATIGRAPHY

2.1 INTRODUCTION

As discussed in chapter 1, the early Middle Pleistocene was an extremely complex time period with a number of larger and smaller scale climatic changes. This study focused on the *Microtus* remains from two important early Middle Pleistocene sites in the UK; Westbury sub-Mendip and Boxgrove. Both sites have complex stratigraphic sequences, covering more than one climatic cycle, and this chapter covers their stratigraphic units, including lithological and sedimentological characteristics, in detail. The evidence for climatic conditions within each unit is also discussed.

The third site included within this study is that of Walou Cave, Belgium. The sediments found at Walou cave are much younger than Westbury and Boxgrove, dating to the late Pleistocene and Holocene. Although the major questions this study aimed to answer are concerned with the early Middle Pleistocene of the UK, relationships between the Walou Cave sediments are extremely well understood and the dating of the stratigraphic units at the site is extremely good, unlike those at Westbury and Boxgrove. Therefore, the Walou cave sequence is included here as a test-site used to evaluate the application of GMM methods to distinguishing *Microtus* remains from different stratigraphic levels, prior to applying them to the less understood early Middle Pleistocene sites. Locations of the sites are shown in Figure 2.1.

Figure 2.1*: Location Map of the three main sites included within this study.*

2.2 BOXGROVE

The former aggregate quarry site of Boxgrove is one of the most important early Middle Pleistocene sites of Europe. Abundant lithic artefacts, belonging to the Acheulean tradition, have been found at the site, many of them in fresh, unrolled condition *in situ*, providing a rare insight into hominin behaviour at this time, including evidence of hunting episodes (Wenban-Smith, 1999; Roberts and Parfitt, 1999). The presence of a partial tibia and two incisors attributed to *Homo heidelbergensis,* further confirmed the importance of the site in the understanding of the early Middle Pleistocene in Europe, as hominin remains of this age are extremely rare (Roberts *et al.*, 1994; Stringer & Trinkhaus, 1999). The deposits at this site date to the period when hominins first appeared in the UK, making it one of the earliest currently known and

these *H. heidelbergensis* remains are currently the oldest human remains from the UK (Stringer & Trinkaus, 1999).

2.2.1 LOCATION

National Grid Reference: SU9208

The Boxgrove site is located in West Sussex, UK, and 12km from the modern-day coastline.

Two quarries were excavated, and the full stratigraphic sequence is present in both (Fig 2.2).

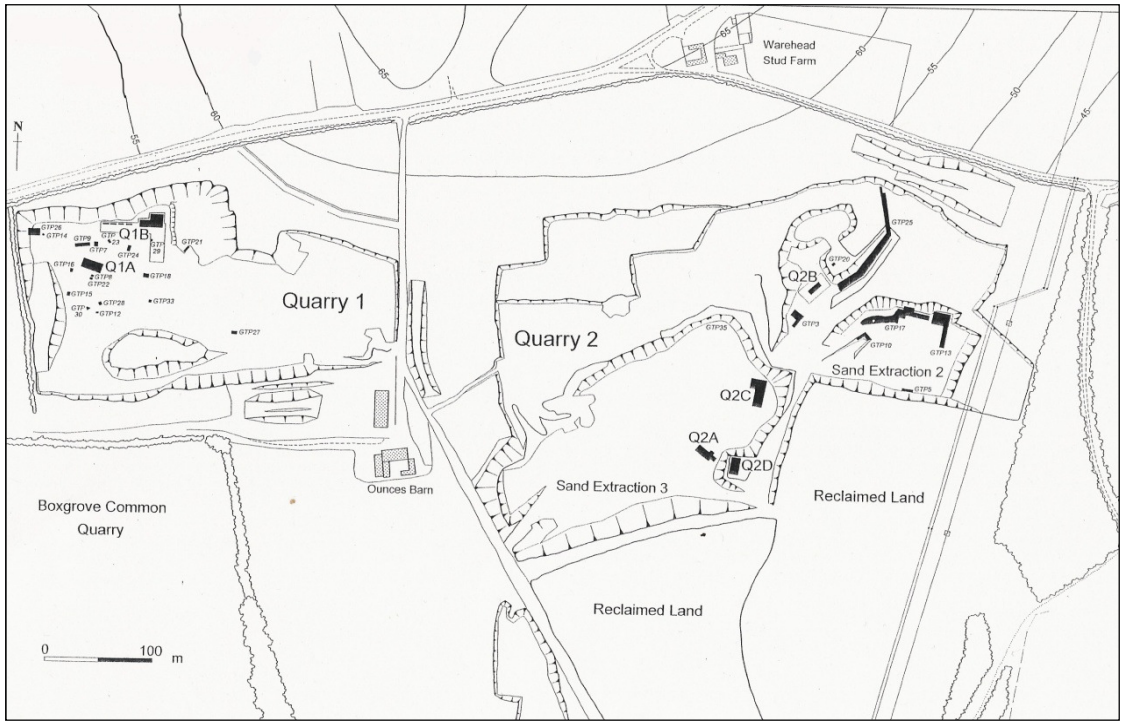

Fig 2.2*: Location of excavation sites (Quarry 1A and B, Quarry2 A, B, C and D) within Boxgrove Quarries 1& 2 (Modified from Roberts and Parfitt 1999 p16).*

2.2.2 GEOLOGICAL SETTING

The Boxgrove stratigraphic sequences comprise marine, lagoonal and terrestrial sediments overlying a marine beach, which is cut into the Upper Cretaceous solid chalk bedrock of the area. The chalk exposed in the Boxgrove excavation sequences mainly belongs to the Tarrant and Spetisbury Members, both of which contain large quantities of accessible flint, which would have been an attractive resource to hominin species for tool making (Roberts, 1999a). The site lies within the West Sussex Coastal plain, an area which experienced a large number of marine transgressions and regressions within at least the last 0.5mya, as a result of successive glacial and interglacial climatic phases. The site at Boxgrove forms the upper part of a sequence of marine terraces, known as the West Sussex Coastal Plain terraces. These terraces represent successive sea-level high stands which have cut into the coastal chalk cliffs. These cliffs have then been elevated due to progressive isostatic uplift, leading to the terraces rising above sea-level and therefore being protected from erosion by successive sea-level changes (Roberts, 1999b). Four marine terraces are recognised within the West Sussex Coastal Plain; Goodwood-Slindon, Aldingbourne, Brighton-Norton and Pagham. Boxgrove is located within the Goodwood-Slindon formation, which is the oldest and highest terrace within the sequence, at 40m OD (above mean sea level), and is dated to approximately 500,000 BP (Westaway *et al.*, 2006).

The exploration history in the Boxgrove area is a relatively long one, with the earliest recognition of raised beach deposits within the region in the early 19th century (Mantell, 1822), the Boxgrove raised beach deposit first being recognised by Prestwich (1859). The first archaeological discoveries at the site were made in 1934, when upper Slindon Formation beach deposits were found to contain handaxes and

the lower Aldingbourne Formation deposits contained flakes and cores. The site is currently within an active sand quarry, and the main period of excavation was the English Heritage funded rescue excavation undertaken from 1983-1993, led by M. Roberts, which aimed to investigate and record the site prior to disturbance caused by quarrying activities (Roberts, 1999a).

2.2.3 STRATIGRAPHIC SUMMARY

The stratigraphic sequence at Boxgrove consists of 2 major units: at the base, the Slindon Formation which is overlain by the Eartham Formation, (see below, fig 2. 3).

The sequence at Boxgrove represents a series of marine events which shaped the landscape and led to a range of sediments representing marine, lagoonal and terrestrial phases being deposited. The Slindon formation comprises three stratigraphic units; the Slindon Gravel Member at the base (beds 1&2), followed by the Slindon Sand Member (Bed 3) and the Slindon Silt Member at the top of the sequence (Bed 4, see Fig 2. 4). Three Marine cycles are represented within the Slindon sand Member. The marine cycles represent phases of high sea level and marine transgression and regression. A period of marine regression is then represented by the Slindon Silts, which were formed due to the lower sea level and the formation of a spur of land which blocked the direct path of the sea into the Boxgrove area, causing a large lagoon or intertidal mud flat area to form. At the top of this sequence, soils began to form once sea-levels fell further (Slindon Soil bed 4c/d).

The Eartham Formation represents the end of the marine influence on the area. After this phase, Periglacial conditions form and large amounts of gravel and mass

movement sediments are deposited at the site (Roberts., 1999b). Relationships between all stratigraphic levels can been seen in Table 2.1.

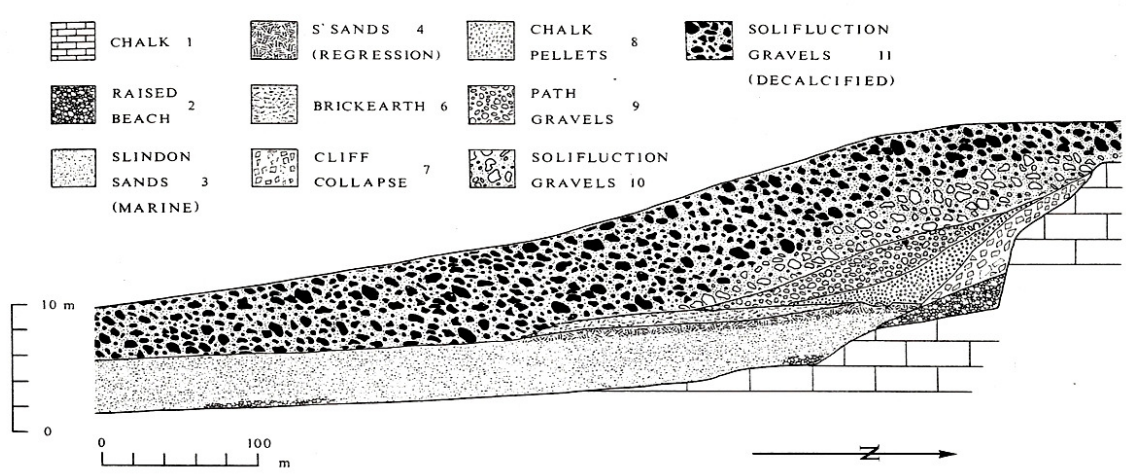

Fig 2.3: *Composite full stratigraphic sequence showing relationships between sediments at Boxgrove (Modified from Roberts 1986 p219).*

2.2.3a SLINDON FORMATION- UNITS 1-5a[1]

The Slindon Formation comprises a series of units at the base of the Boxgrove stratigraphical sequence, representing the raised beach deposits.

The Slindon Gravels are the basal sediments at the site and represent marine flint shingle beaches.

[1] Note: All sedimentary descriptions for Boxgrove are from Roberts and Parfitt (1999) and all descriptions for Westbury are from Andrews et al.(1999) unless otherwise stated. .

The Slindon sands are next in the sequence and were laid down by tidal processes at a time of high sea level. The sands display features which suggest that they are a

mixture of nearshore, subtidal and intertidal deposits, and therefore represents the three separate marine cycles, indicating three phases of transgression and regression.

The Slindon Silts represent an increasingly protected environment over time, with a lagoonal environment forming, allowing the deposition of silts in shallow water, leading to soil formation occurring during periods of low water levels.

The sediment source for these deposits appears to be the Tertiary deposits of the Lower Coastal Plain and the Cretaceous chalk bedrock that underlies the site.

UNIT 1- Slindon Gravel Member.

The Slindon Gravel Member is made up of a medium to coarse sand matrix containing flint gravel, ranging from well rounded to angular, with all levels of modification being represented. Fracturing of the clasts is common, suggesting frost damage and a high energy environment which represents the cutting of the platform into the chalk by the sea.

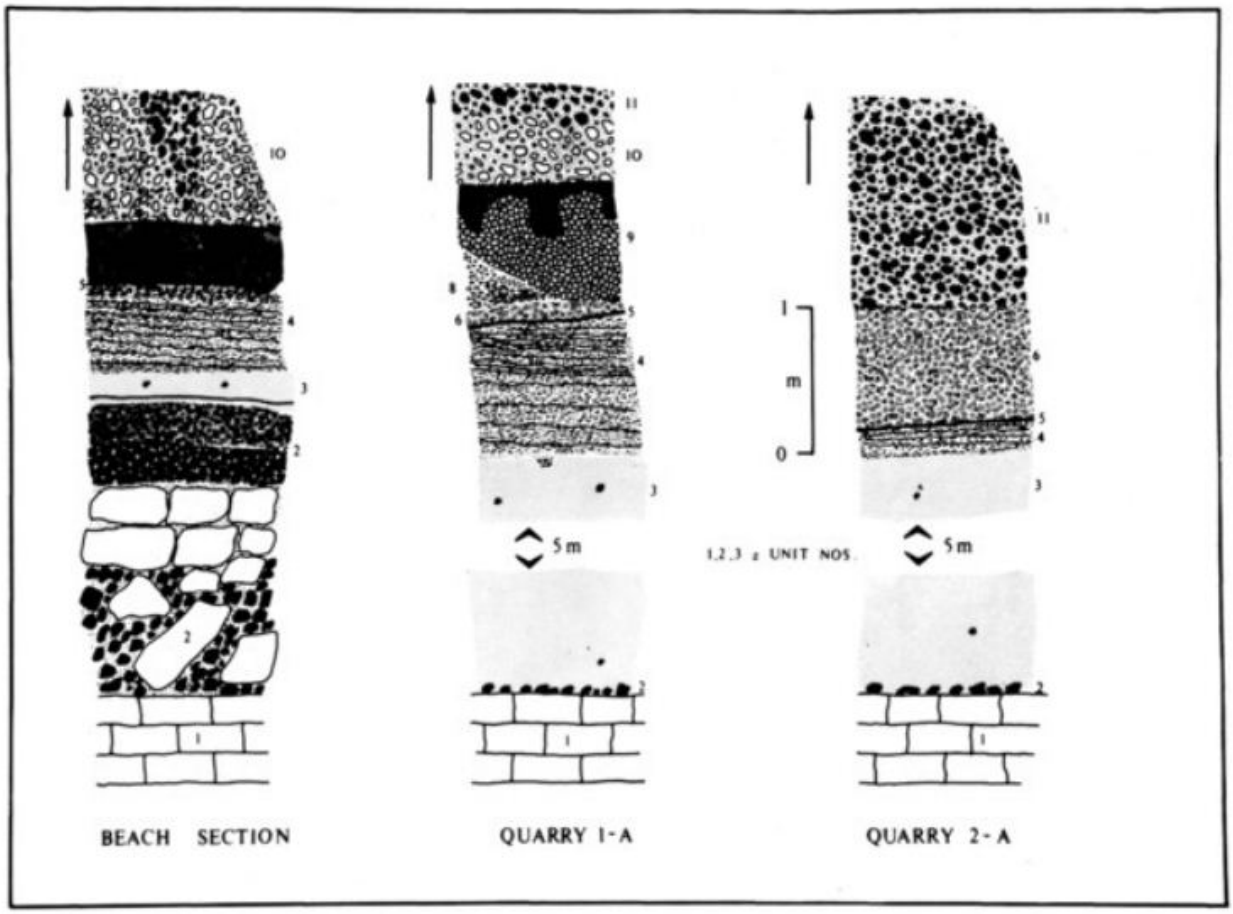

Figure 2.4: *Stratigraphic sequence at Boxgrove showing relationship sections (Modified from Bergman et al., 1998; p108). See table 2.1 for detailed stratigraphy.*

Stage	Formation	Member	Unit Numbers	Informal Bed designations (GTP25)
Anglian/Elsterian	Eartham Formation	Eartham Upper Gravel Member	Unit 11	Upper Head gravel Upper Silt Bed Upper Middle Head Gravel Middle Silt Bed Lower Middle Head Gravel Lower Silt Bed Lower Head Gravel
			Unit 10	Calcareous Head Gravel
			Unit 9 - Path Gravels	Fan Gravel Beds
		Earham Lower Gravel Member	Unit 8- Upper Chalk Pellet Be	
			Unit 6- Brickearth Beds	
			Unit 5b, 5c- (GTP 17 only)	
			Unit 8- Lower Chalk Pellet Be	Chalk Pellet Beds
			Unit 7- Angular Chalk beds	
Cromerian IV	Slindon Formation	Slindon Silt Member	Unit 5a- (Fe/Mn Horizon)	Organic Bed
			Unit 4c and 4d (Q1 only)	Slindon Soil Bed
			Unit 4b	Lagoonal/ Intertidal Beds
			Unit 4a	
		Slindon Sand Member	Unit 3	Marine Cycle 3 Marine Cycle 2 Marine Cycle 1
		Slindon Gravel Member	Unit 2	Beach Gravel Beds
			Unit 1	

Table 2.1: Detailed stratigraphic sequence at Boxgrove showing relationships between units, members and formations, Informal beds are shown for GTP25 only. Reduced sediment diversity was observed at GTP 5 & Q2/A- see Roberts & Parfitt (1999), p32 for further details.

UNIT 2- Slindon sand Member

Unit 2 lies directly on top of the Unit 1 gravels. It is anomalous in that it is composed of clays with fine sand, followed by sequential composite bedding, which becomes increasingly coarse into strongly cemented clay displaying few depositional structures and containing occasional gravel particles. This sequence of sediments is thought to represent intertidal mudflats passing into mixed flats and then high velocity waves in shallow water, followed by the accumulation of a sandbar then finally alternating intertidal and storm beds.

UNIT 3- Slindon sand Member

Unit 3 represents the three marine cycles discussed above, and is composed of nearshore and intertidal fine-grained marine sands

UNIT 4- Slindon Silts

The change of the Slindon Formation from sands to silt shows a change in the local environment surrounding the site from an open coastline into a more protected, low-energy environment. The silts were laid down as intertidal mudflats in a lagoonal type environment. At least one major land surface is present within the Silts, suggesting that the silt surface was exposed long enough for soil to form.

Unit 4 accumulated during the terminal stage of marine cycle 3, and the silty sediments which characterise this unit are present at most excavation locations, although not all facies are identifiable at all locations.

Unit 4a is highly variable across the different excavation areas, although the basic composition of the sub-unit is of thinly laminated, wavy, horizontally bedded mud and silt. Strong basal erosion is evident, with coarser elements such as shell fragments and flint pebbles included as lag. Fine sand deposits occur within the laminations close to the shoreline, and further off-shore where Mollusca are also common. Bioturbation is present throughout much of the unit; however, it is rarely strong enough to have disrupted the primary bedding structures. The unit as a whole appears to represent an intertidal mudflat within a lagoonal or estuarine environment.

Unit 4b is also a silt to fine sand laminated sequence, with wavy bedding. Bioturbation is low throughout the unit and coarse elements such as large shells and gravel have been rafted by seaweed and deposited. The environment suggested by these sediments is again of an intertidal mud-flat in an estuarine or lagoonal setting.

Unit 4c is essentially a massive mud deposit; however there are remains of some depositional features, such as laminated sediments preserved within the sub-unit, suggesting that post-depositional factors have affected the unit and removed many of the original features. Bioturbation by plant and animals (including some terrestrial animals), along with chemical alteration, appear to have been the main causes of this. This makes the identification both of the top and bottom of this unit difficult, as areas where laminations have survived could belong to either those levels above or below unit 4c. However, enough information survives to show that this unit represents the transition from marine to a terrestrial environment. Both bone and flint artefacts are present within this unit.

Unit 4d mainly occurs in Q1/B and consists of a series of finely laminated pond marls with occasional calcareous ‘soil’ remnants which were rich in calcite and fossils, and

were probably associated with a calcareous spring feature (Roberts *et al.*, 1994; Macphail, 1999).

UNIT 5- Slindon Silt Formation/ Eartham Upper Gravel Member

Unit 5a is allocated to the terminal phase of the Slindon Silt Formation, although, units 5b and 5c are present at GTP 17 where they are found significantly higher in the sequence and are part of the Eartham Upper Gravel Member.

The boundary between 4c and 5a is difficult to discern as 5a has also been greatly affected by post-depositional processes. The unit is made up of laminated silts, sands and mud, and iron and manganese banding is present throughout the unit, suggesting an increased organic content (Macphail, 1999).

2.2.3B THE EARTHAM FORMATION- UNITS 5B-11

Unit 5b is composed of chalky marl consisting of finely laminated chalky clay at the base containing small chalk pellets derived from the weathering of the surrounding chalk cliffs, possibly while temperatures were cooling and humidity was increasing. Terrestrial molluscan remains are present within this sub-unit, which is thought to represent wide shallow terrestrial pools.

Sub-unit 5c is composed of narrow, mottled dark brown sand with some silt containing large quantities of mammal and worked lithic remains. The unit possibly represents reworked material washed in from 5b (Macphail, 1999).

UNIT 6- Brickearth

At the base of unit 6, there are wide, non-parallel laminated silts and clays, followed by cross bedded silt/ sand units. In site Q2/a, there is also a third sub-unit consisting of rhythmites, laid down in shallow pools of still water.

Unit 7-Chalk Cliff Collapse

This stratigraphic level is restricted in location to immediately above the pebble beach. The matrix is made up of white, chalky clay, surrounding large angular blocks of limestone and black flint nodules. The unit is interpreted as being deposited when blocks of chalk collapsed from the cliff.

UNIT 8- Chalk Pellet beds

The Lower chalk pellet bed occurs only at GTP 25 and consists of thick layers of chalky debris contained within a pale chalky mud. Chalk clasts become smaller and more rounded towards the top of this sub-unit.

The upper chalk pellet bed has a highly distorted lower boundary made up of very well rounded chalk pellets in a pale chalky mud matrix.

UNIT 9- Fan Gravel Beds

Unit 9 comprises well sorted sub-rounded fine flint gravel with a brown silty matrix, the matrix becoming absent towards the base, with the matrix-free clasts displaying heavy manganese staining. The flint is thought to have been stripped from the northern cliff wall, having been previously altered then reworked into this unit rather than having been rounded during the accumulation of this unit.

UNIT 10

Unit 10 consists of weathered remains from the cliff, which has been soliflucted and transported by slope processes.

UNIT 11

Traces of cold-soil development are seen in this horizon, which consists of soliflucted tertiary regolith with fine bands of silt. It is similar in composition to unit 10, both representing mass movement gravels.

2.2.4 PALAEOENVIRONMENTAL INTERPRETATION

The excellent recovery of mammalian, reptile, amphibian and avian remains at Boxgrove means that a detailed palaeoenvironmental reconstruction of the site has been possible (See Currant, 1999; Gentry, 1999 and Turner, 1999 for in-depth analyses of mammalian species at the site.). Palaeoenvironment and climate were inferred primarily from taxonomic index scores, which infer the climate of past species through the range of habitats in which they are found in the present day (see Evans *et al.*, 1981 for further detail).

2.2.4A: SLINDON FORMATION PALAEOENVIRONMENTAL RECONSTRUCTION

Faunal remains are relatively uncommon in the lower units of the Slindon formation (Unit 3, Slindon Sand member and Units 4a and b, Slidon Silt member). While marine faunal remains are common, terrestrial faunal remains are particularly uncommon within the Slindon Sands as this member represents a marine environment. However, the Slindon Silt member has sparse terrestrial faunal remains, including *Microtus subterraneus, Apodemus sylvaticus* (wood mouse), *Capreolus capreolus* (roe deer) and

Felis silvestris (wild cat). The presence of these species suggest that the environment at Boxgrove during the time the Slindon Silts were being deposited was of dense vegetation or woodland and a temperate climate, although the climate was likely to be cooler than the present day, as indicated by the higher proportion of boreal and tundra species than found in Central and Western European forest at the present day.

Unit 4c, the Slindon Soil Bed, contains an abundant vertebrate fauna, including large and small mammals. The mammalian remains suggest there was a mosaic of habitats within the vicinity of the site. The presence of grassland is indicated by *M. subterraneus, M. agrestis, M. arvalis and Arvicola t. Cantiana*. The presence of *Apodemus sylvaticus* (Woodmouse), *Dama dama* (Fallow Deer), *Meles* spp. (Badger) *and Clethrionomys glareolus* (Bank Vole) suggest there was also a woodland habitat close to the site. These species are all found in temperate climatic conditions in the present day and it appears the environment at Boxgrove during this period was of temperate deciduous forest or mixed woodland and grassland.

Unit 4d is thought to represent a pond contemporaneous with unit 4c. Remains in this unit are dominated by fish and water birds are also common. Small mammal remains recovered from the unit, including *D. dama* (fallow deer) and *Stephanorhinus hundsheimensis* (extinct Rhinoceros) support the suggestion that the climate and habitats were similar to that found in unit 4c.

Vertebrate remains from unit 5a, the Organic Bed, are very similar in composition to those from unit 4c. However, there is a slightly larger proportion of boreal and tundra species within this unit. Overall, the habitat reconstruction is similar to that of unit 4c, a mosaic of wood and grasslands in a temperate climate. However, the larger

proportions of tundra and boreal species suggest that the climate may have been cooler than that of the other Slindon member units.

2.2.4B EARTHAM FORMATION PALAEOENVIRONMENTAL RECONSTRUCTION

The Eartham Lower Gravel Members (units 7-8) are rich in small mammal remains with Roe Deer the only large mammal species recovered. Overall, the species representation and therefore the climatic and habitat reconstructions are similar to that of unit 5a.

By contrast, the Eartham Upper Gravel Member contains evidence for cold conditions in unit 6'3, immediately overlying unit 5a. Species present within this unit that suggest a cool, boreal forest environment include *Microtus oeconomus* and *Myopus schisticolor* (wood lemming). Immediately above this layer, unit 6'3'Fe contains *A. c. terrestis, M. subterraneus, M. agrestis* and *M. arvalis*, which suggests a return to a warmer, more temperate woodland environment.

Unit 5b

Unit 5b, the Calcareous Marl, contains a fauna, including *Lemmus lemmus* (Norway Vole) and *Canis lupus* (wolf), which suggests cold, open conditions.

Unit 6: Brickearths

Unit 6 contains *Clethrionomys rufocanus* (Grey-sided Vole), *Lemmus lemmus* and *M. gregalis,* which suggests this unit represents cold, open grassland conditions with the presence of some woodland cover being indicated by the presence of the European

Beaver (*Castor fiber*) and the bank vole (*Clethrionomys glareolus*) suggesting that some woodland was present near the site.

Overall, the vertebrate fauna at Boxgrove suggests a warm, temperate climate with areas of both woodland and grassland which then cooled throughout the sequence to become a cold, more open environment.

2.3 WESTBURY SUB-MENDIP

Westbury-sub-Mendip is one of the largest and oldest cave-system sites containing mammalian remains known within the UK. The site covers both temperate and cool climatic phases, and each stratigraphic level contains a distinctive and often extremely abundant mammalian fauna, representing a diversity of mammal species and depositional environments, ranging from a cave-bear denning area, to a bird of prey roosting site. The abundance of the mammalian remains and the presence of several different climatic phases within the sequence mean that the site at Westbury is of particular importance in understanding the history of the early Middle Pleistocene in the UK.

Flint 'artefacts' from unstratified levels at the site were initially identified by Bishop (1974), however, the Natural History Museum excavations (1976-80), which recorded many stratified flints and re-examination of Bishop's 'artefacts', could not find a single

unequivocal humanly produced artefact (Cook,1999), although whether or not there are artefacts from the site remains a controversial topic. A cut-marked red deer metacarpal, from unit 19, suggests some human activity within the general vicinity of the site at the time in which the sediments were laid down (Andrews, 1999). As the site consisted of a series of very steep sink-holes into a deep cave system, it is unlikely that human occupation occurred within the cave, but the presence of cut-marked bone within the cave is important, as it provides evidence of one of the earliest known human occupation periods within the UK (Cook, 1999).

2.3.1 LOCATION

The quarry site of Westbury sub-Mendip is located at the southern edge of the Mendip Hills (NGR 506 504) and is 213-244m OD (above standard sea level) in elevation. The Mendip Hills run in excess of 30 miles, from Weston-super-Mare to the Bristol Channel. The rocks formed in the late Carboniferous period when the Upper Palaeozoic sediments of the area were subjected to faulting and folding.

The site consists of the partly exposed infilling sediments of an extensive Limestone cave system, visible in the NE corner of the quarry (Stanton, 1973; 1999).

The Westbury sediments are extremely rich in vertebrate remains, particularly cave bear (*Ursus deningeri*) and small rodent remains, including *Microtus*. The mammalian fauna from Westbury is extremely important. The remains recovered from the Siliceous Member were relatively rare, and are likely to have been derived from a wide source area, and possibly represent a long time period, meaning that the remains recovered from the unit cannot be considered a 'fauna'. However, the remains from the Calcareous Member accumulated over a relatively short time period and were

derived from the local area, and therefore hold much information about the environment and climate at the time during which they were deposited.

2.3.2 EXCAVATION HISTORY

Three major periods of excavation and recovery of remains have occurred at the Westbury site, beginning in 1969 when the area was opened up as a Limestone extraction quarry. Mammalian remains from the site (mainly large bones and teeth) were discovered by quarry workers at the site, and were then identified and examined at Bristol City Museum. Further controlled collection and recording was then undertaken by E. Tratman in the same year. The importance of the site was recognised at this time, and the need for further excavations was suggested (Heal, 1970).

The first in-depth study of the site h was undertaken by Mike Bishop in 1972-74, when he collected large amounts of both large and small mammalian, reptile and avian remains and recorded many stratigraphic sections that no longer survive due to blasting activities at the site. Bishop also reported the finding of many flints that he considered to show evidence of human working, placing hominins at the site for the first time (Bishop, 1974, 1982). Bishop also suggested that the site represented a new, previously unidentified interglacial period, situated between the Cromerian and Hoxnian stages (Bishop, 1982).

The Natural History Museum (British Museum) then took on further excavations at the site in 1976-1984, revealing much further evidence relating to the age and taphonomic history of the site and producing an excellent photographic and sedimentological record of the site. The stratigraphic information below is taken from the NHM

monograph on the Westbury site, unless otherwise noted, as the greater resolution and detail available in these sections replaces previous work (Andrews *et al.*, 1990).

2.3.3 STRATIGRAPHIC SUMMARY

The stratigraphic sequence at Westbury is an extremely complex one, further complicated by the fact that many of the sequences recorded by Bishop (1982) were destroyed by the quarry company prior to the Natural History Museum (NHM) excavations which began in 1976, therefore correlations between stratigraphic levels recorded in the two excavation reports are in many cases impossible

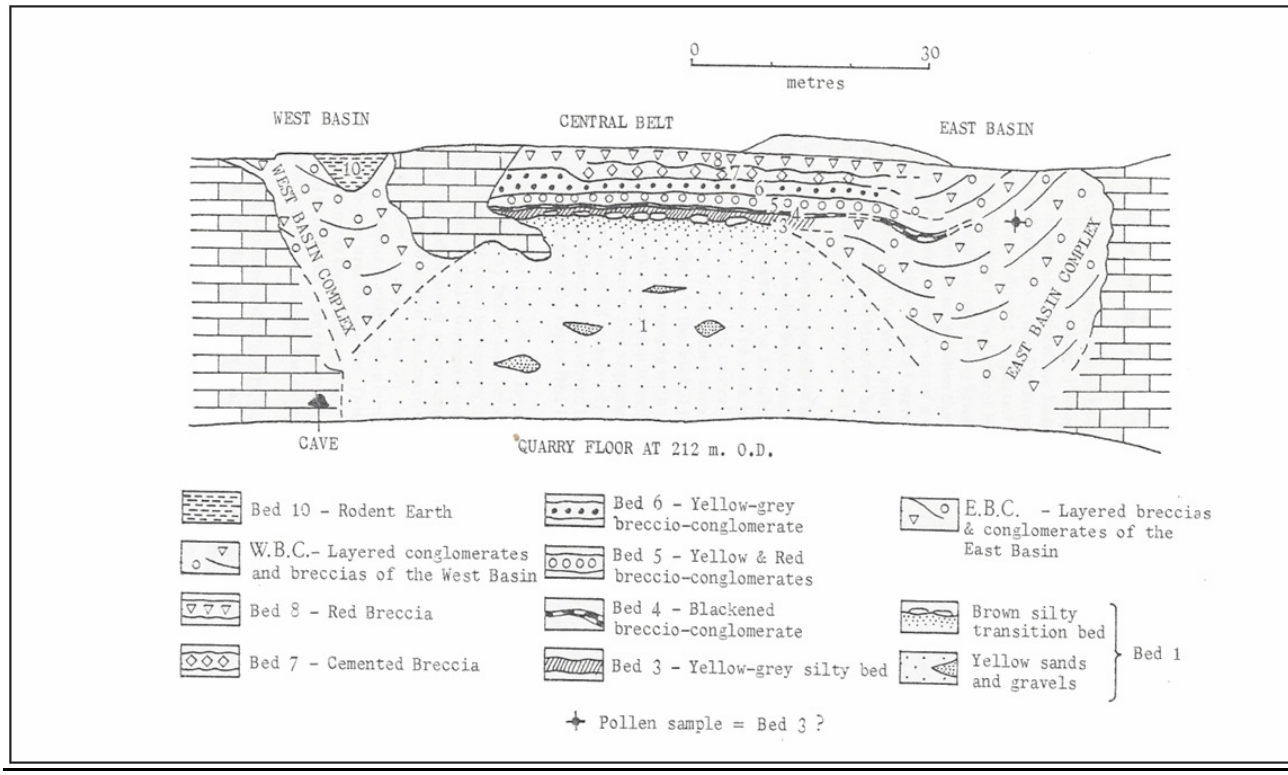

Figure 2.5: *Bishop's interpretation of the Westbury Stratigraphic Sequence (Modified from Bishop, 1982 p 18).*

The units described by Bishop (198, fig 2.5) were largely contained within the destroyed central complex of the cave, whereas the NHM excavations concentrated

upon the accessible areas in the remaining East Basin Complex and the West Basin Complex. Due to the steep and unstable nature of many of the Westbury deposits, several different areas were excavated where conditions allowed.

In the NHM excavations, no direct equivalents to many of the units described by Bishop were recorded, due to their being missing, no longer accessible in the steep and dangerous quarry face, or simply unrecognisable as being the same sedimentary unit due to changes in composition over the lateral extent of the site or taphonomic factors. Further complications arose due to the fact that Bishop's excavations and collection of material was extremely spatially limited, meaning that his stratigraphic control and resolution was limited compared to the NHM excavations. Due to the problems described above, no definitive complete stratigraphic sequence combining both sets of excavations exists. The NHM excavations recorded 19 stratigraphic units and at least 60 sub-units, highlighting the complexity present at the site. However, it is hoped that the study of the *Microtus* remains contained within the site may begin to test and verify the inferred stratigraphic sequence of the sediments.

Westbury is an isolated site, with no known regional correlatives, probably due to the fact that the Mendip landscape is one that has been subjected to large amounts of re-excavation due to glacial and fluvial action.

Two different chambers were identified within the Westbury cave system- the main chamber (=Strike chamber, Bishop, 1974, fig 2.5) which runs parallel to the strike of the Limestone bedrock and the side chamber. The northern extreme of the main chamber was exposed at sites W1 and W4. The southern wall of the cave was destroyed by quarrying activities, although some remnants could be seen at W10. The

extent of the main chamber, as suggested by the exposures available in the NHM excavations, is 60m length by 25m width and 30m depth (Fig 2.6).

The side chamber is located to the North West of the main chamber and although the exact dimensions are not known, it is significantly smaller than the main chamber. The side chamber appears to have formed in a different way from the main chamber, and the sediment source appears to have been from the North and East, compared with the South and East for the main chamber.

The stratigraphy at Westbury in all areas of the site is split into 2 broad units; the higher Calcareous Member and the lower Siliceous Member.

2.3.4 MAIN CHAMBER UNITS

2.3.4A SILICEOUS MEMBER

The Siliceous Member consists of over 15m of pale yellow fine sands and gravels.

The bedding throughout the unit is variable, from well-bedded bands 3-4mm thick to uniform bands up to a metre thick. Gravel lenses occur at random intervals throughout the unit. The bedding is disrupted by grading and cross-bedding. These features are characteristic of water-lain sediments and contortions and faulting observed throughout the sediments suggests slumping and settling of the sediments after deposition. Limestone fragments at the top of the unit suggest a partial collapse of the Limestone roof of the cave system. The unit is thought to have been laid down under a period of glacial conditions, with the sediments being lain down during the summer melt water streams (gravels) and snowfield melt waters (sands).

The material from which the Siliceous Member is formed is not typically found within the local area in the present day and, therefore, must represent material which has

been transported from a significant distance, then deposited within the cave system. Several different methods have been suggested to explain the mode of transport of the material making up the Siliceous Member, as summarised below;

Stanton (1973) believed that the absence of typical Mendip rocks suggested that the rocks making up the Mendip hills had not yet been uplifted and forced into the range of hills which exist today, placing the Siliceous Member sediments within the deep past. However, the presence of undeniably Pleistocene mammal faunas within the deposits filling the cave system, including the Siliceous Member, proves this not to be the case (Bishop, 1982). Bishop suggested that the cave system formed due to a Pleistocene.

Surface stream flowing south across the surface of the plateau, washing sediments into the cave and cutting through the blanket of Jurassic rock that covered the plateau and into the limestone underneath, forming the Westbury cave system.

However, Currant (1999) believed this explanation also to be incorrect, as for the stream to have run across the surface of the plateau, the ongoing exhumation of the Jurassic sediments overlying the Limestone would have had to leave a layer of impermeable mudstone covering the plateau for long enough for the cave complex to form, which is highly unlikely. Currant (1999) suggested that the more parsimonious explanation for the exotic origin of the sediments making up the Siliceous Member is that the transporting melt water stream was approaching the Mendips from the south, rather than exiting the Mendip range, flowing from a source to the north and exiting the range to the north, as previous authors had assumed.

Siliceous Member Main Chamber Units

UNIT 1

The Siliceous Member was poorly exposed within the main chamber during the NHM excavations.[2] During Bishop's excavations however, the Member was present.

[2] All sedimentary sequence descriptions are referenced to Andrews *et al*, 1999, unless otherwise stated.

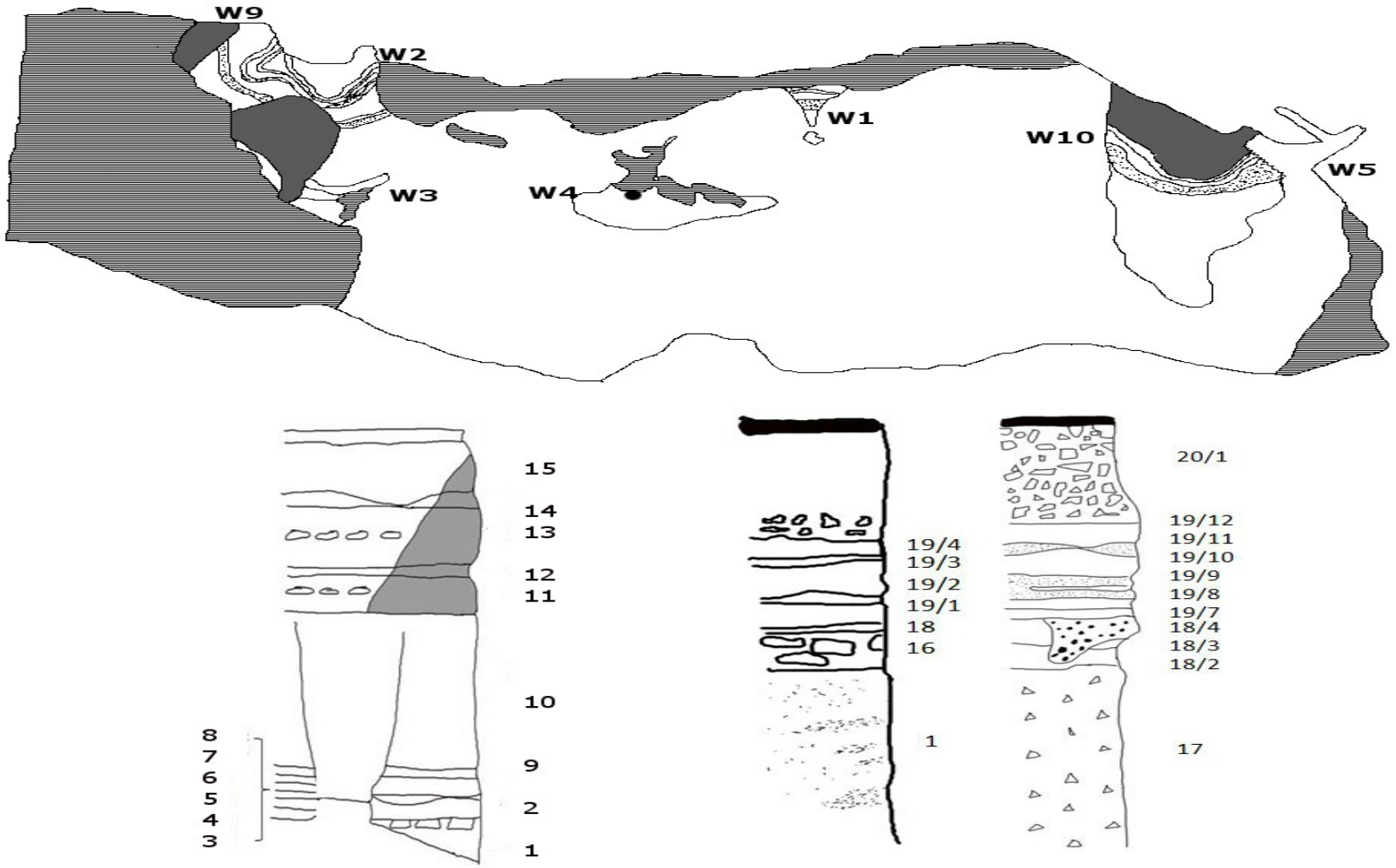

Figure 2.6: Composite drawing of Westbury Cave showing location of excavation sites and their stratigraphic sequences. (Modified from Roberts and Parfitt, 1999).

3.3.4B CALCAREOUS MEMBER

The Calcareous Member lies directly on top of the transitional layer representing the partial roof collapse in the Siliceous Member.

All authors agree that the discontinuity between the Siliceous and Calcareous Member represents a significant cessation in sedimentation within the cave complex. It is not possible to determine the length of this break, although climatic conditions appear to have changed significantly into warmer, more temperate conditions.

UNIT 17

Unit 17 is found at the eastern most extent of the cave exposure, below sites W10 and W5 at site W11, where they replace the Siliceous Member. Unit 17 consists of a series of uncemented and loosely consolidated reddish brown and brown breccias measuring a maximum of 15-20m thick. Limestone clasts consolidate the unit, with silty or sandy deposits interspersed in the gaps between the clasts. At the base of the unit, clasts are mainly angular; however, towards the top of the sequence, they become more heavily altered, with clasts becoming more rounded. Stratification within the unit, however, is mainly present in the form of colour rather than sedimentological changes. These sediments replace the Siliceous Member at site W11.

UNIT 18- Grey Breccia

Unit 18 is present throughout the main excavated areas within the main chamber, at sites W5, W10 and W1 and also at W11. They overlie the sediments of unit 17 at site W11 and the Siliceous Member sediments at the other sites. Unit 18 consists of abundant Limestone clasts, of variable angularity, with a silty grey matrix and

abundant fossil bones. The unit is highly variable between the different excavated locations.

Site W1 has rounded to sub-rounded clasts at the base of the unit, which are often blackened and are surrounded by a silty olive brown matrix with occasional chert inclusions. The clasts become more altered and frequent higher up the section, and the matrix becomes dark grey/brown in colour with a few fossil bones present throughout the unit.

At site W10, changes throughout the unit are more defined than those at W1, leading to division into several sub-units. The lowest sub-unit, 18/2, contains fewer heavily altered smaller clasts within a dark grey/ brown silty matrix. Unit 18/ 3 occurs after a gradual transition, and contains a greater quantity of small clasts, which are less heavily altered than those in sub-unit 18/2. The overall quantity of clasts also increases. The colour of the matrix is lighter at this level and fossil remains are more abundant and well preserved than at W1. Unit 18/4 is described as a cobble bed, which consists of a self-supporting mass of heavily cemented cobbles and pebbles with little or no matrix present. The cobble bed replaces the grey breccia laterally, with steep-sided transitions between it and the grey breccia to the east and west. The clasts and bone remains are of the same composition as the lateral equivalents within the grey breccia, and the feature is thought to represent compaction of units 18/2 and 18/3 after the matrix was washed away, resulting in slumping of the deposits.

At site W5, the grey breccia appears to be similar to subunits 18/2 and 18/3 as present at site W10, although it is more heavily cemented. Unit 18/6 at this site is thought to be equivalent to 18/3 at W10.

Above the grey breccia at this site, a yellow/ red silty breccia is present as an intrusive feature (subunit 18/7); consisting of less heavily altered Limestone which is well cemented. It is capped by a gravel bed (subunit 18/8), which consists of a thin, continuous bed of blackened pebbles, which is also present at site W10 as subunit 18/5.

Unit 18 is thought to correlate with Bishop's bed 3 and possibly bed 4.

UNIT 19 – Yellow Breccias

Unit 19 is present at W1, W5, W10 lying above the Grey Breccias, and consists of a series of yellow breccias interstratified with red silts. Several sub-units are present within the yellow breccias, (19/6, 19/2, 19/8, 19/10, 19/12, 19/4, 19/17) and all are composed of a self-supporting rounded limestone clast framework, with a matrix consisting of a brown/yellow to yellow medium silt to fine sand component. Occasional limestone clasts are heavily weathered and chert inclusions are common. Bone is locally abundant, although always damaged either prior to deposition or *in situ,* due to pressures from the surrounding sediments.

The silty red sub-units (19/5, 19/3, 19/1, 19/14, 19/11, 19/16) are brown to yellow/red in colour and thinner than the yellow breccias.

UNIT 20- Red Breccia

Unit 20 is present within the main chamber at sites W10 and W5. At these locations, the top of the sedimentary sequence was formed by fresh, angular Limestone blocks fallen from the roof of the cave and a thick, red poorly sorted breccia. Bones are present but not frequent throughout the entirety of this unit.

2.3.5 SIDE CHAMBER UNITS

UNIT 2- Grey and Red Breccias

The Grey and Red Breccias are located within site W3 and lie directly on top of the Siliceous Member. The grey and red breccias are composed of several sub-units. (2/1-2/3)

UNIT 3

This is a red/brown breccia found within the W3 extension consisting of sub-rounded Limestone clasts and a fine silty matrix. No bone is present within this unit.

UNIT 4

This is a yellow/ brown waterlain silt found within the W3 extension, containing a low concentration of heavily altered and rounded Limestone clasts. Clear colour banding is present within the silty matrix. No bone is present within this unit.

UNIT 5- Crushed Bone layer

This unit consists of unaltered angular limestone clasts and a clay/silt matrix. Gravel and crushed bone are also present within discreet areas of this unit. The colour and composition of the unit is extremely variable; the colour varies from yellow to olive and red. The bone component within this unit is composed entirely of cave bear, as in sub-unit 2/2; however the bone is more heavily broken within this unit.

UNIT 6- Red and Yellow Silts

Unit 6 is found above the crushed bone layer and is laterally equivalent to unit 2, in unit W3. It comprises red silt containing sub-angular Limestone blocks and more heavily altered limestone clasts. Gravel, sand and crushed bone is present within the unit, with the bone and limestone showing evidence of weak acid etching caused by solution. However, outside of the gravel relatively complete bone is present and fairly common.

UNIT 7

This is a finely bedded waterlain yellow silt, found within site W3, possibly representing a short ponding episode between the accumulation of units 7 and 8.

UNIT 8

Unit 8 has a limited exposure in the W3 extension between two boulders. It is similar in composition to unit 6, although in comparison to unit 6, the limestone clasts are less rounded. Gravel mixed with black stained bone is also present within this unit, containing mainly small mammal remains, although some bear remains are identifiable.

UNIT 9

Unit 9 is located above the grey and red breccias in W3 and is composed of Calcitic silt, containing no bone, with silt and gravel components derived from decomposed speleothem.

UNIT 10- Yellow Silty Breccia

Overlying unit 9 in W3 and 3 to 8 at W3 extension is unit 10, a red/ yellow breccia consisting of silt to fine sand, containing only slightly altered medium-sized limestone clasts. This unit is up to 5m thick in places, and is almost completely uncemented, except near the walls of the cave where limestone clasts are far more abundant. Bones are relatively rare, except at the top of the unit, where fossils, particularly of bats, occur in pockets.

UNIT 11- Pink Breccia

Found at W2 and W2/9, this unit is highly variable, both in composition and colour, with several sub-units identified throughout the sites.

11/1 Sub-Unit 11/1 is located within the W2/9 sequence and comprises a yellow/red breccia matrix containing limestone boulders, cobbles and pebbles, which are angular to sub-angular in condition. Bone of both small and large mammals is present and well preserved.

11/2 Unit 11/2 is part of the W2/9 sequence and is a red-brown level made up of recemented rotten stalagmite. Clasts are infrequent, but those which do occur are angular-sub angular limestone pebbles and cobbles. Bone is present, although the preservation is variable, with some specimens being described as rotten whereas others are in good condition.

11/3 The sediments in unit 11/3 are mottled white, black and brown rotten stalagmite remains containing pebble and cobble angular limestone clasts located within the W2 sequence. Small bone fragments and small mammal remains are present.

11/4 Sub-unit 11/4 is a yellow-red breccia containing abundant well-preserved mammalian remains, with a concentration of large bones across the middle of the bed. Limestone clasts are boulder to pebble in size and sub-angular.

UNIT 12- Dark Brown Breccia

This unit consists of a dark brown fine sand/silt matrix containing uncommon limestone clasts which are angular and minimally altered, found in units W2 and W2/9. Bones are present throughout this unit and are stained red/ brown. The sub-units present at W2 (12/1) and W2/9 (12/2) are very similar in composition; however, 12/2 contains a greater percentage of limestone clasts and bone material, and manganese staining is also present within this sub-unit.

UNIT 13- Brown Breccia

Unit 13 is a highly variable unit, found throughout W2/9, and therefore it is not possible to define sub-divisions within it, despite the unit being over 2m thick. It consists of a large self-supporting mass made up of large sub-angular to minimally altered limestone clasts surrounded by a red/brown silty matrix. It also contains a concentration of large limestone boulders c. 30cm from the base, which may represent a partial collapse of the cave roof. Small quantities of fragmentary bone is present throughout the unit, with a concentration of small mammal remains being found approximately half way through the unit near the western cave wall.

UNIT 14- Silty Grey Breccia/ Grey Silt

Unit 14 is found within W2 and is an extremely distinctive unit, consisting of a yellow/brown to grey/brown breccia to the west, becoming variable in thickness and

changing laterally into pure silt at the bottom of the solution feature. Small Limestone clasts are present within the unit.

UNIT 15- Red Breccia/ Red Silts

This unit has extremely similar stratigraphic features to unit 14, in changing from a breccia to the west into silt at the W2 solution feature. Several sub-units have been identified within W/2 and W2/9;

15/1 and 15/3 Lower Breccias

15/1 is present at the W2/9 site and is a yellow/red breccia, containing boulder, cobble and pebble limestone clasts with some chert, which display a small amount of rolling. Microfaunal remains are abundant at this level.

15/3 is present at the W2 site and consists of yellow/red silt containing angular chert pebble clasts with infrequent, fragmentary mammalian remains.

15/2 and 15/4- Dark Silts. Sub-unit 15/2 is located in the W2/9 sequence and is a red silty breccia, containing mainly limestone clasts with a small proportion of flint. Clast condition is variable, ranging from minimally to heavily rounded. Mammalian remains are present within this level, and are abundant in some areas. 15/4 is located in the W2 sequence and is dark brown- red silt. Mammalian remains and clasts are sporadic and poorly preserved within this level. This unit appears to represent the remains of a solution feature. Both sub-units are thought to represent the equivalent stratigraphic level.

15/5, 15/6, 15/7- Intermediate Silts. All of the intermediate silts are located within the W2 sequence. Sub-unit 15/5 is a yellow-red silt, containing some angular chert gravel. Bone is locally preserved in pockets within the unit.

15/6 is a red-yellow layer composed of rotten stalagmite remains containing angular chert pebbles. Bone is not preserved within this level.

15/7 is a dark brown-yellow red unit composed of cherty silt containing sporadic angular pebble clasts and rare mammalian remains.

15/8- Rodent Earth Sub-unit 15/8 contains abundant small mammal remains, which are well preserved but often fragmentary. The unit matrix is yellow-red bone gravel with some angular to rounded chert pebble clasts.

15/9- Red Silt 15/9 is a red silt, only known as a solution remnant with sporadic chert pebbles. Mammalian remains are absent from this level.

UNIT 21

Unit 21 is a matrix of angular clasts containing no bones, which is banked against the northwest Limestone wall of the cave level with units 10-13. Correlation of this unit with the stratigraphic sequence is unclear, and the unit may represent an erosional remnant, or an infilling in a space left by erosion of older units.

UNIT 22- Infill deposits.

Unit 22 separates W3 and W3 extension and is made up of a mass of unconsolidated breccia sediments, probably representing infill caused by a massive collapse feature.

2.3.6 PALAEOENVIRONMENTAL RECONSTRUCTION

Unit 11 within the calcareous Member has a thermophilious Chiropteran (Bat) assemblage suggesting a fully temperate interglacial environment. This is further confirmed by the presence of *Dama dama* (fallow Deer), *Apodemus sylvaticus* (wood Mouse) *and Clethioromys glareolus* (bank Vole), which at the present day prefer temperate broad-leafed woodland.

Units 13, 14 and 15/1 contain faunal elements such as *Cricetulus migratorius* which represent a significant decline in the climate to continental conditions from that shown in unit 11. Unit 13 in particular appears to contain boreal and steppic elements. However, these faunal elements do not represent a fully interglacial fauna- the micro mammals present within the assemblages such as *M. gregalis* are found in areas with have continuous soil cover and unfrozen ground, suggesting sub-optimal interglacial conditions.

Unit 15/2, 15/4 are equivalent and contain species such as *C. elaphus*, and *C. glareolus* that represent a shift in climate to a second temperate optimum with a habitat of mixed deciduous woodland.

Unit 15/18 includes several steppe/ tundra micromammalian species, including *M. oeconomus*, *M. gregalis* and *Lemmus* within the faunal assemblage at this level, suggesting a return to peri-galcial conditions.

2.4 WALOU CAVE

2.4.1 LOCATION

Walou Cave is located in southern Belgium, approximately 10km south-east of Liege. The site is located on the Magne River, a tributary of the Vesdre. The cave is cut into Visnean limestone bedrock and contains a sequence of well-preserved, largely continuous, stratified deposits dating from the Middle Pleistocene to the Holocene (Dewez, 2008).

2.4.2 EXCAVATION HISTORY

The cave site at Walou has been subjected to intensive study for many years, making it one of the best understood cave sites within Belgium. Initial excavation at the site was undertaken by the *Société wallonne de Palethnologie* (SoWaP) between 1985 and 1990 (Dewez *et al*., 1993). Sedimentary and stratigraphic analyses were undertaken at the site during this time period (See Chen *et al.*, 1988; Collcutt, 1993, Lacroix 1993). Palaeoenvironmental interpretation of the site and description of the faunal remains from the SoWaP excavations were also published at a later date (Pirson & Toussaint, 2002). A second stage of excavation commenced between 1996 and 2004 (Draily, 1998, 2004). This stage of excavation allowed further refinement of the stratigraphic sequence at the site (Pirson *et al.*, 2004) and during this excavation, a Neanderthal tooth was also recovered (Draily *et al.*, 1999), underlining the importance of the site within the reconstruction of the Middle Palaeolithic in Belgium.

2.4.3 STRATIGRAPHIC SUMMARY

Within the Walou Cave sedimentary sequence, there are 4 main units: A, B, C and D, covering a long time sequence from MIS6-1 (c.120-5kya). Such a long, continuous stratigraphic sequence is rare within the Pleistocene and Holocene of Europe, and Walou Cave is particularly important due to stone tools in many of the stratigraphic levels, accompanied by both large and small mammalian remains. Unless otherwise referenced, all stratigraphic summary information within section 2.4.3 is adapted from Pirson *et al.* (2006).

2.4.3A UNIT D

Unit DII is poorly documented and is the basal unit at Walou cave, overlying the limestone bedrock. The unit consists of sand and silt layers containing very few limestone clasts.

Unit DI contains two layers of pale yellow-brown silt with limestone blocks at the base, followed by three soil horizons showing evidence of strong pedogenesis in the form of ghosted limestone clasts and carbonate concretions. Evidence of Middle Palaeolithic activity at the site in the form stone tools has also been recorded at this level**.**

2.4.3B UNIT C

Unit C is split into six main sub-units (CV-C0) which all contain an abundance of coarse elements, particularly limestone clasts. The unit C sediments form a continuous sequence from c. 115-26Kya.

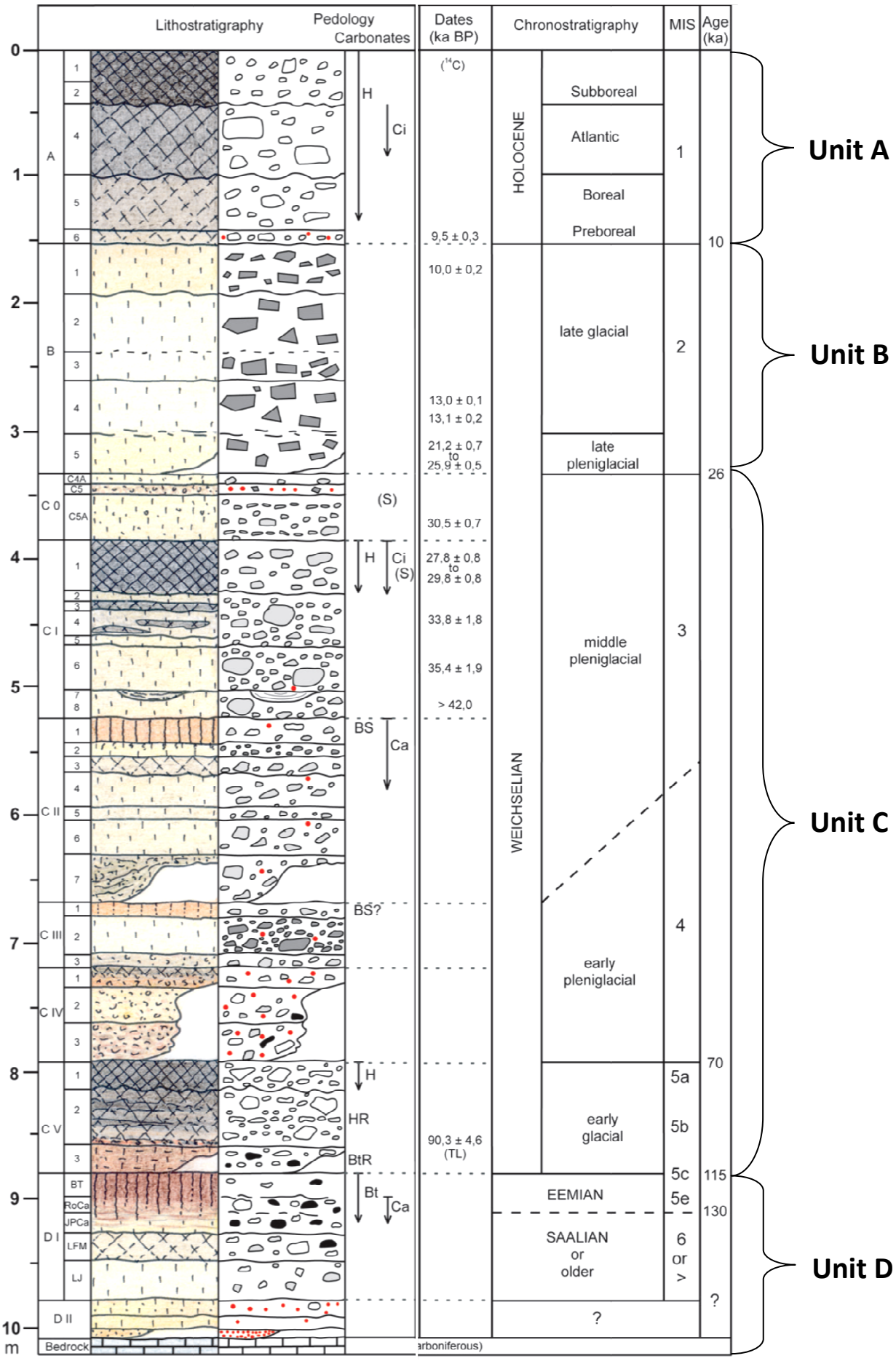

Figure 2.7: Walou cave Stratigraphy (Modified from Pirson *et al*, 2006)

Unit CV consists of 3 sub-units. Unit CV-3 lies directly on top of unit D1 and was developed in a small channel as a result of re-working of the underlying sediments. The matrix is red-brown silt containing limestone clasts, which are in very variable condition, from rolled to angular. No artefacts have been found within this unit,

Unit CV-2 is a reworked humic palaeosol containing strongly altered limestone clasts, charcoal lenses and middle Palaeolithic tools. A Thermoluminescence date from this unit dates it to approx. 90.3Kya (±4.6 Kya).

The CV1 matrix is made of compacted dark brown silt, containing strongly altered limestone clasts, interpreted as being the in-situ remains of a humic palaeosol. Middle Palaeolithic tools have been found within this level.

Unit CIV consists of the remains of a channel feature which was eroded into the underlying levels. The matrix (CIV1-3) which fills this channel feature consists of heterogeneous orange-brown to dark brown silts, some sub-rounded, re-worked small limestone clasts and some re-worked Middle Palaeolithic lithic artefacts.

Unit CIII is composed of 3 sub-units (CIII-1 to 3). Unit CIII-3 is a hetrogeneous silt layer, formed due to re-working of the underlying sediments. This unit is followed by CIII-2, which is a grey-yellow silt formed by re-working of loess. Limestone clasts are present within the matrix. Middle Palaeolithic artefacts have been found within this sub-unit. CIII-1 is a compact, clayey red-brown silt formed by a partly re-worked palaeosol.

Unit CII is very similar in structure to CIII. CII-7 is a hetrogeneous silt layer, formed due to re-working of the underlying sediments. This unit is followed by units CII-6-4 which are grey-yellow silt formed by re-working of loess. Unit CII-6 contains some laminated

sediments CII-3 is a layer or brown silt, followed by CII-2 is again, a grey-yellow silt formed by re-working of loess.

CII-1 is a compact, clayey red-brown silt formed by a partly re-worked palaeosol. In-situ carbonates covering limestone blocks at the top of this level suggest that the uppermost part of the sequence is undisturbed. All units within CII contain Middle Palaeolithic artefacts.

UNIT CI comprises sub-units 8-1. Sub-units CI-8 and 6-2 are beige to dark brown heterogeneous silt. Levels CI-8 and CI-6 contain Middle Palaeolithic artefacts and CI-8 also contained a Neanderthal tooth and is ^{14}C dated to >42Kya. C1-7 is a small channel feature cut into the underlying unit CI-8. The channel is filled with a stratified, silty matrix. CI-1 is an in-situ humic palaeosol made up of thick, dark brown clayey silt, ^{14}C dated to 27.8-29.8Kya (±0.8Kya). Unit CI-1 contains the first evidence of modern human activity at the site, in the form of Aurignacian stone tools.

2.4.3C UNIT B

Unit B consists of 5 sub-units and is quite different, both geometrically and lithologically from the underlying units. There is an angular unconformity between unit B and the uppermost sediments of unit C. Unit C is largely composed of heterogeneous yellow silt containing very few limestone clasts. Those clasts which are present within the matrix are angular and not corroded, which is a marked difference from the clast-heavy maxtix of units D and C. Rhizoliths at the B2/B1 boundary suggest there may have been a truncated palaeosol at this level. Sub-unit B5 is more orange in colour than the other units and contains Gravettian artefacts and is ^{14}C dated to c. 21.2-25.9 Kya. (±0.6Kya). The following unit, B4, contains Magdelenian artefacts and is dated to c. 12Kya. The uppermost level within unit B, B1, is also slightly more orange

in colour and contains Epipalaeolithic artefacts; ^{14}C dates at this level suggest that it is c. 10Kya.

2.4.3D UNIT A

Unit A consists of 6 silty sub-units which become darker towards the top of the sequence, changing from orange-brow to dark brown. The units also become progressively more granular towards the top of the unit. Rounded, corroded clasts are common within the whole of this unit. Mesolithic tools are found in units A4 and 5, with Neolithic tools being excavated from A2. The base of the unit is dated using 14C to 9.5Kya (±0.3Kya).

2.4.4 PALAEOENVIRONMENTAL RECONSTRUCTION

Several palaeoenvironmental reconstructions have been put forward for Walou Cave. Cordy (1991, 1993), Turmes (1996) and Dewez (2008) looked at the mammalian faunas from individual units within the sequence. Parfitt and Stewart (2010) have provided an overview of the palaeoenvironmental reconstruction of the full sequence when the modern environmental ranges of the small mammal taxa found at Walou cave is related to the environmental conditions at Walou Cave, as described below;

Unit D contains a mixture of woodland and dry continental taxa, including *Clethrionomys sp*. and *M. gregalis.* However, due to difficulties in separating the faunas from DII and D1, it is not possible to tell if this represents a contemporary faunal assemblage or if the two units have different climatic and habitat conditions.

Unit CV contains species that indicate temperate interstadial conditions

Unit CIV appears to be a cold level, although the presence of a minor temperate component within the assemblage suggests that the conditions may have been cooling rather than fully cold.

Unit CIII contain an assemblage including species which indicate cold, open grassland existed around Walou cave at the time.

The palaeoenvironmental reconstruction for unit CII is complex. The basal unit CII-7 yields a small mammal assemblage which indicates that there were very severe cold conditions and an open grassland habitat surrounding Walou cave, containing some dry and some wet areas.

CII-6 has a similar assemblage to CII-7, although there is a lack of species that prefer wet conditions, suggesting that the environment was dry and cold.

CII-4 – Throughout the CII sequence, conditions appear to be ameliorating, with a decline in arid and cold adapted species. The small assemblage from CII-4 contains *M.arvalis* and *M. oeconomus* suggesting wet grassland and cool conditions.

CII-2- This level contains too few mammalian remains to provide an accurate climatic and habitat reconstruction,

CII-1 Yields a similar assemblage to CII-4, although the presence of *Sorex. caecutiens* and another, unidentified *Sorex* species suggests the vegetation was very dense.

Unit CI

CI-8 to 6. The small mammal assemblage at these levels provides evidence for interstadial conditions with a coniferous woodland habitat, similar to Northern coniferous woodlands today, close to Walou Cave. Indicator species include *M. arvalis,*

M. oeconomus (which prefers wet conditions), *M. subterraneus,* which lives today in grassland and deciduous forest, and a *Dicrostonyx* species.

Levels CI 5 to 3 contain very few small mammal species and, therefore, the environment cannot be reconstructed fully. However, the presence of *Lemmus sp*. And *M. gregalis* in higher numbers than in CII levels suggests that these units may indicate a cooling of the climate.

At level CI-1, small mammal remains were extremely abundant, and dominated by dry grassland rodents such as *M. oeconomus*, *M. arvalis* and *Arvicola terrestris*. Mole remains (*Talpa* spp.) were present in large numbers within this level, which suggests that the ground was not frozen. *Sorex araneus*, also present within this unit, prefers deciduous woodland. Therefore, it appears that this level indicates a return to interstadial conditions.

Unit B

B5- Conditions similar to those of CI-1 are indicated at this level by the presence of species including *M. arvalis, M. oeconomus* and *Arvicola terrestis* and abundant mole remains. Therefore, the climate at this time was humid and mild but not fully temperate.

In comparison with the underlying levels, in units B4 to2- *D. torquatus* and *M. gregalis* are the most common small mammals present. This suggests an abrupt climatic shift to severe cold conditions and an open habitat. In unit B1, there is a mix of cold and temperate-adapted species, which may suggest that the small mammal assemblage is not all contemporaneous. However, the cold adapted-species such as *Lemmus* and *Dicrostonyx* spp. are present in relatively small numbers, whereas temperate dense

vegetation preferring species such as *Clethrionomys* and *Apodemus spp.* dominate the assemblage.

CHAPTER 3
INTRODUCTION TO THE TAXONOMY OF MICROTUS

3.1 INTRODUCTION

This study aimed to explore the dental morphology of four *Microtus* species from the British Pleistocene, to gain further understanding of their taxonomy and species identification, and to improve the use of Pleistocene *Microtus* remains for dating and palaeoenvironmental reconstructions.

This chapter introduces the evolutionary history of the genus *Microtus* and examines the dental morphology, habitats and distribution of the four *Microtus* species included within this study; *M. arvalis, M. agrestis, M. gregalis* and *M. subterraneus*.

3.2 THE GENUS MICROTUS

The genus *Microtus* comprises a widespread group of small-eared voles, belonging to the sub-Family of Arvicoline rodents, which are found throughout Europe, North America and Asia. They are characterised by their permanently-growing complex molars, which are an adaptation to their presence in grassy areas and their diet of grasses, grains, roots and barks (Guthrie, 1965). Although well over fifty species of *Microtus* are known worldwide, this study will concentrate upon the four most common species in the British Pleistocene: *Microtus agrestis* **(**short-tailed field vole, Linnaeus, 1781), *Microtus arvalis* (common or Orkney vole, Pallas, 1778), *Microtus*

gregalis (narrow-skulled vole, Pallas, 1779) and *Microtus subterraneus* (European pine vole, de Selys-Longchamps, 1876).

Fossil specimens of the genus *Microtus* provide an important resource for palaeontologists and evolutionary biologists to help piece together past environments, population histories and genetic links. *Microtus* species display extremely rapid dental evolution over the last two million years, faster than any other mammalian group, with the same amount of evolution occurring during the Pleistocene as seen in the entire Palaeogene and Neogene (c.65.5-5.5 Mya) in other groups (see Guthrie,1965, Chaline et al, 1999).

This rapid dental evolution is of particular interest to palaeontologists, as teeth are more resistant to chemical decay and breakage than bone. Even when the voles are directly predated, Microtine rodent molars are very resilient to destruction, and therefore are frequently preserved as fossils (Hillson, 2004). Andrews (1990) studied the effects of taphonomic processes upon small mammal remains at Westbury-sub-Mendip and found that teeth are the skeletal element most resistant to factors such as decay, breakage and damage through acid erosion from the stomachs of birds of prey. At most levels in the site, rodent teeth are the most abundant skeletal element, with an estimation of between c.35 and 95% of the original specimens remaining, as compared with .5-30% for more easily broken elements such as long bones (as calculated through Minimum Number of Individuals of the most common skeletal element). Therefore, dental remains survive well within the palaeontological record, making studies of evolutionary change over long periods possible, including the potential to track both morphological change and geographical movement throughout the Pleistocene.

Mammalian teeth are known to be resistant to epigenetic effects upon tooth morphology, meaning that they are particularly useful in the reconstruction of phylogenetic relationships (Hillson, 2004). Uhlĭkovā (2004) has shown that in *M. arvalis* there is no effect of epigenetic factors upon the shape of the M_1, as morphological differences in the shape of the M_1 and M^3 between populations did not reflect the epigenetic differences observed in the same populations.

The rapid dental evolution seen in *Microtus* species means that the remains are useful in the dating of sites using biostratigraphy, with the presence or absence of certain species or morphological characteristics of a species ('morphotypes') providing at least the basis for initial relative dating of a site. This method is of particular importance for sites beyond the boundary at which radiocarbon dating becomes unreliable (c. 40 Kya) or in sites where different dating methods may produce conflicting results.

3.3 EVOLUTION OF *MICROTUS*

The evolution of the Arvicolidae is thought to have occurred approximately 5Mya, with the evolution of *Microtus* within the Arvicolinae occurring in Central Europe in the Middle Pliocene at approximately 1.2Mya (Martin and Tesakov, 1998; Maul & Markova, 2007). There appears to have been an Arvicoline radiation from their area of origin in the Arctic Ocean borderland into Eurasia at approximately 2.2Mya. These species, which belonged to the genus *Allophaiomys,* radiated across Eurasia and into North America, being one of the few small mammal genera to enter the New World via the Beringian land bridge. By 1Mya they had a range which extended from the Atlantic coast of North America to Europe *(*Repenning *et al*., 1990). The name *Allophaiomys* has been used to describe a group with a large geographic range covering Europe and

Russia during the Lower Pleistocene (1.8-1.5 Mya)**,** which probably represents a large group of closely related species. Some of these species, such as *A*. *Deucalion* (Van der Meulen, 1974) and *A*. *pliocaenicus* (Kormos, 1932), are thought to represent the earliest ancestors of *Microtus* (Nadachowski & Zagorodnyuk. 1996).

The genus *Allophaiomys* is defined by the following characteristics:

1. Molars without roots

2. The presence of crown cementum

3. The M_1 consists of three basic triangles and a simple anteroconid complex

4. A simple M_3 with 2 closed triangles and a posterior loop with distinct LRA3

The genus also shows a pattern of dental enamel differentiation from negative-undifferentiated- positive as all species evolved over 1Mya (Martin & Tesakov, 1998). *Allophaiomys* is thought to have evolved from an older genus, (*Mimomys),* characterised by unspecialised rooted teeth (Graphich & Nadachowski, 1996). The suggested relationship between *Allophiomys*, *Mimomys* and *Microtus* can be seen in Fig 3.1. The evolution of *Pitymys* (where the T4 and T5 are confluent) to *Microtus* (with T4 and T5 closed and alternating) morphotypes is characterised by the addition of triangles to the anteroconid complex (Chaline & Graf, 1988).

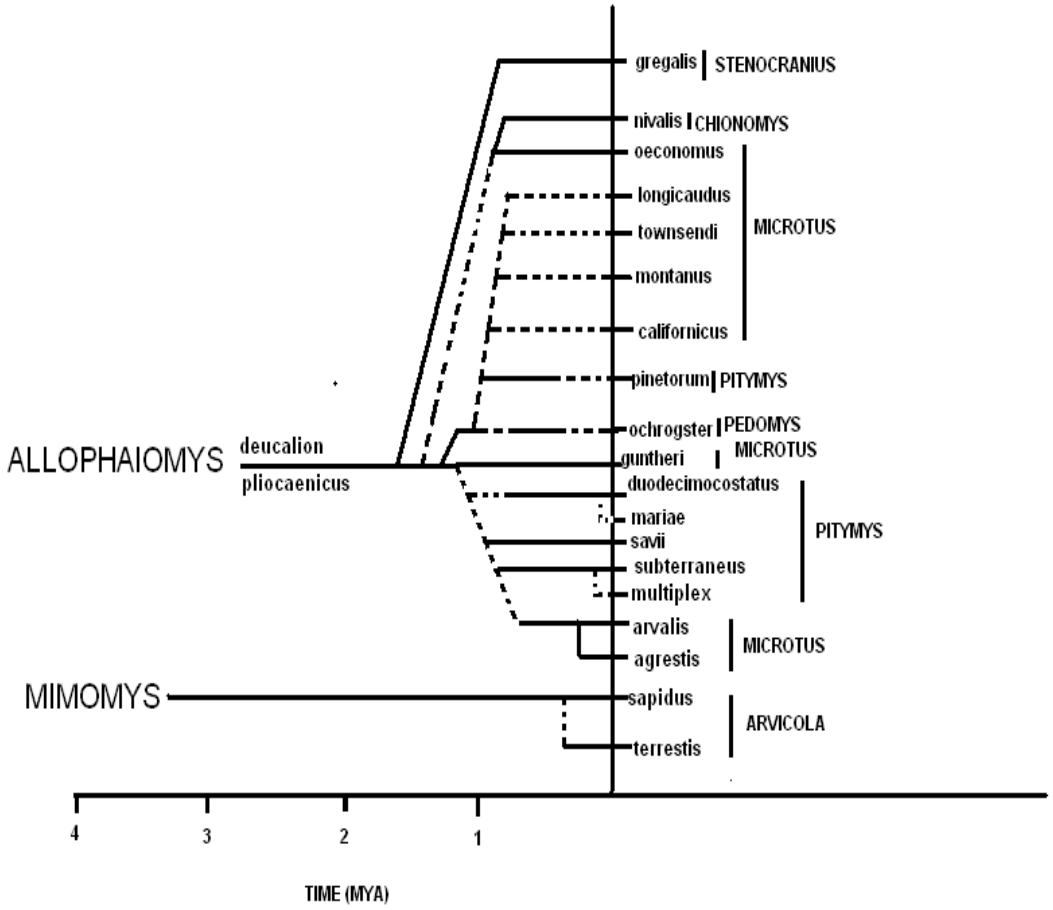

Figure 3.1*: Dendrogram based upon biochemical and morphological analysis of fossil Arvicolinae. Dotted lines represent a speciation event (modified from Chaline and Graf, 1988).*

More recent DNA work by Jaarola *et al.* (2004) supports the view held by Chaline and Graf and separates the five *Microtus* species examined in this study into several distinct groups. *M*. *arvalis* and *M*. *agrestis* appear to have evolved along the same lineage originally, but separated relatively early in the evolution of *Microtus,* although they remain closely linked. *M*. *(stenocranius) gregalis* appears to be widely separated from the *M*. *arvalis*/ *agrestis* grouping (Figure 3.2) An early, rapid radiation appears to have occurred at c. 2Mya, creating the major sub-genera (*Agricola*, *Neodon*, *Microtus*, *Terricola* etc) followed by further rapid evolution within the groupings, resulting in a wide variety of extinct and extant species (Gutherie, 1964; Repenning et al, 1990).

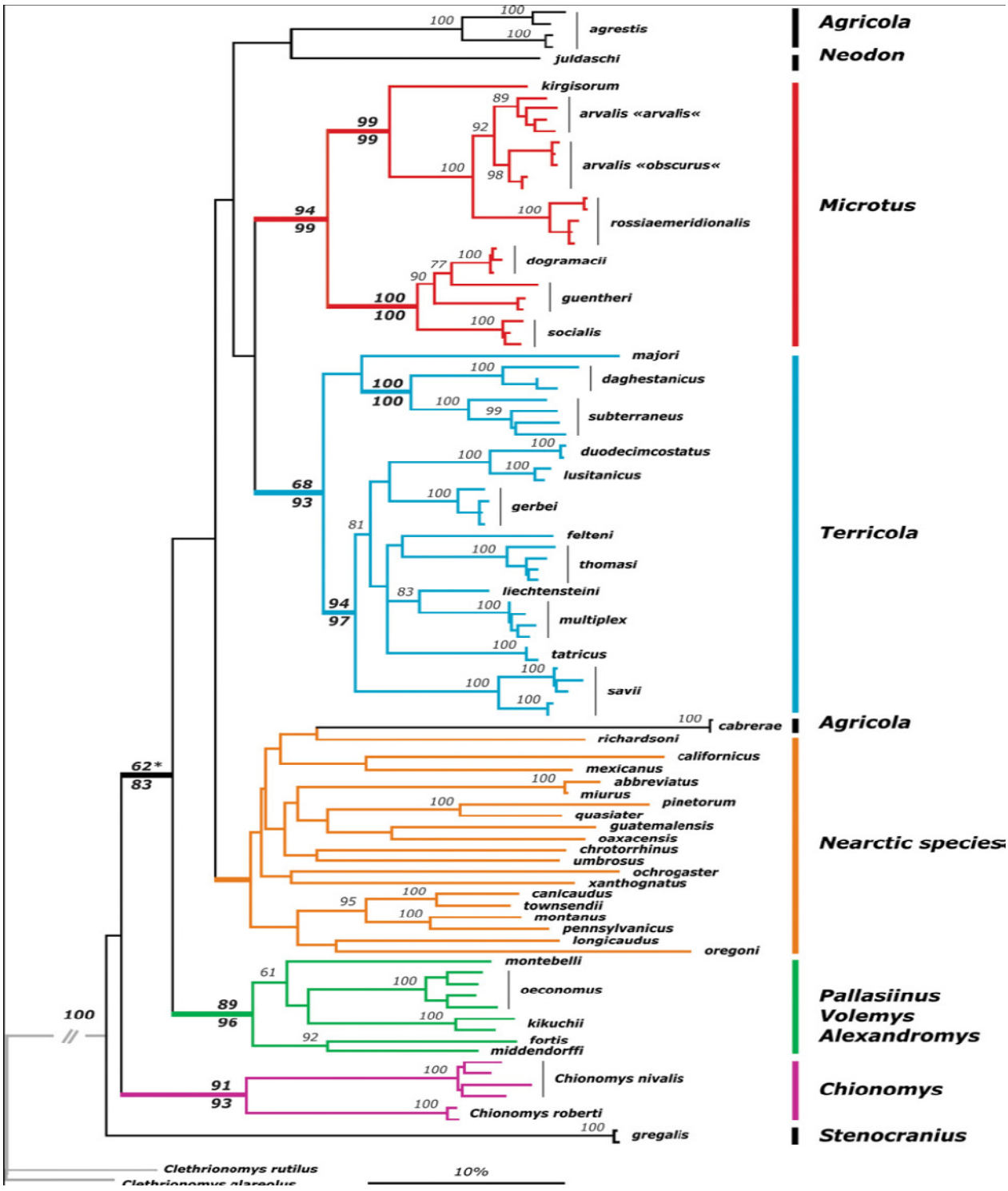

***Figure 3.2**: DNA maximum likelihood analysis of modern Microtus remains (Jaarola et al., 2004).*

3.4 CLASSIFICATION OF MICROTUS

Hierarchy

Kingdom: *Animalia* (Linnaeus, 1758)

Phylum: *Chordata* (Bateson, 1885)

Class: *Mammalia* (Linnaeus, 1758)

Order: *Rodentia* (Bowdich, 1821)

Family: *Cricetidae* (Rochebrune, 1883)

Subfamily: *Arvicolinae* (Gray, 1821)

Genus: *Microtus* (Schrank , 1798)

Synonyms

1798 *Microtus* (Schrank)

1817 *Mynomes* (Rafinesque)

1836 *Hemiotomys* (de Selys-Longchamps)

1857 *Paludicola* (Blasius)

1857 *Agricola* (Blasius)

1867 *Praticola* (Fatio)

1867 *Sylvicola* (Fatio)

1890 *Campicola* (Schultze)

1894 *Tetramerodon* (Rhoads)

1896 *Microtus* (Miller)

1899 *Arvicola* (Acloque)

The genus *Microtus* belongs to the sub-Family Arvicolinae. The Arvicolinae includes voles, lemmings and muskrats and the family is currently Holarctic in distribution.

Microtus dentition consists of three upper and three lower molars in each tooth row, and a pair of long curved incisors (Figure 3.3).

The typical *Microtus* dentition can be described using the following (Figure 3.4);

Upper

M^1 - anterior loop, followed by 4 alternating closed triangles.

M^2 - anterior loop, followed by two internal and 1 external triangles

M^3-anterior loop, three alternating triangles, followed by a posterior loop containing at least 1 deep re-entrant fold (Ellerman, 1940).

Lower

The lower dentition of *Microtus* is the reverse of the upper dentition.

M_1- anteroconid complex, followed by 5 alternating triangles and a posterior loop

M_2- 4 alternating triangles followed by a posterior loop

M_3 -2 or 3 alternating triangles followed by a posterior loop

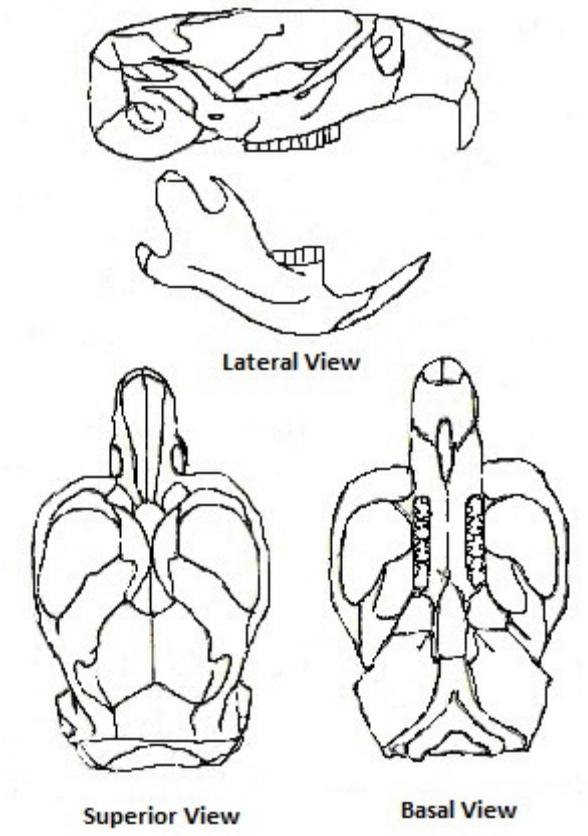

Figure 3.3: *A generalised Microtus skull (adapted from Miller, 1912).*

Microtus teeth can become quite complex, and deviate from this typical dentition via the addition of salient angles ('triangles') to the posterior margins of the upper teeth and the anterior margins of the lower, making the posterior loop of the M^3, and notably the anterior loop of the M_1, the most variable regions of the teeth (Guthrie, 1965).

All morphological descriptions of teeth in this study use the criteria laid down by Van der Meulen (1976), as shown in Figure 3. 5.

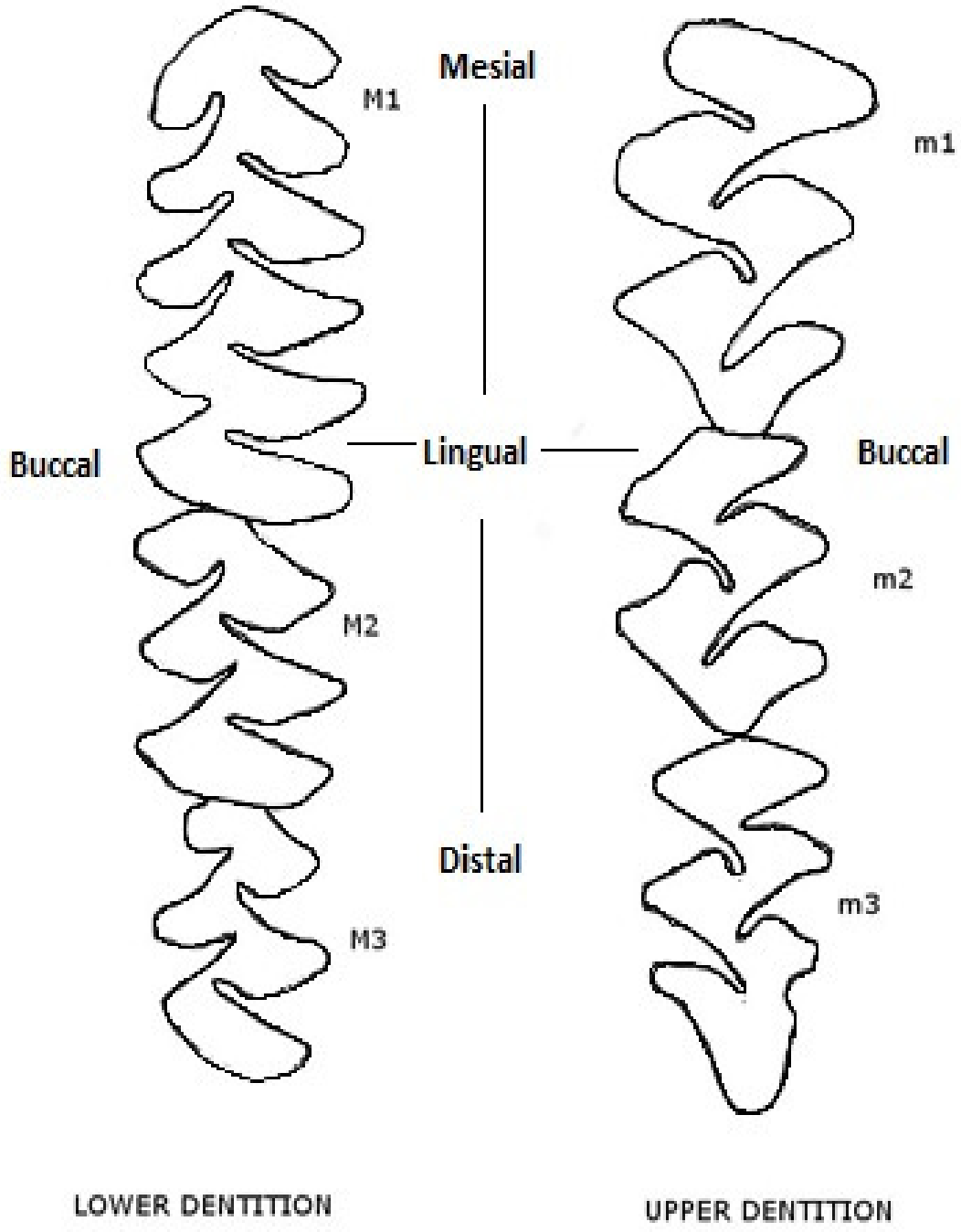

Figure 3.4: *Schematic diagram of generalised Microtus dentition.*

Figure 3.5: *Descriptive definitions of regions of Microtus teeth. (Adapted from Van der Meulen, 1976)(T= triangle, B= Buccal, L= Lingual, SA= Salient angle, RA= Re-entrant angle, PL= posterior loop, AL= anterior loop, AC= anteroconid complex)*

The thickness of the enamel may also be used when describing teeth and can be an important factor in determining the species in *Microtus*. Enamel differentiation and thickness are described using the criteria laid down by Martin (1987) as follows:

Positive- Posterior (trailing) edges of triangles on lower molars are thinner than the anterior (leading) edges.

Negative- Posterior edges of triangles on lower molars are thicker than the anterior edges.

Undifferentiated- both posterior and anterior edges on lower molars are of equal thickness.

Identification of palaeontological *Microtus* specimens is complex, as modern specimens are often identified by zoologists purely on the basis of soft-tissue features which are not preserved in the fossil record. Furthermore, the extremely rapid change in the shape of dentition displayed by *Microtus* species can make comparison difficult between modern examples and ancient ones in an incomplete fossil record.

The identification of past species using their skeletal and dental morphology must always be treated with caution, as a grouping derived through morphological means may in fact represent a grouping of closely related species, which cannot be differentiated through their dental morphology alone (Kowalski, 1992). DNA analysis of remains can differentiate closely grouped species with similar morphology, to a much greater degree than morphological methods may be able to. However, these caveats do not mean that morphological analysis of past species is not a valuable source of information- it is often the only means of analysis available when examining past species, and many valuable conclusions may be drawn from such analyses. Analysis of morphology is of particular importance in material which is more than 50-70,000 years old, as often DNA analysis is most often impossible in specimens which are of that age, due to degradation of DNA over time (Taylor, 1987). However, an understanding that some of the complexities of genetic variation and change will not be represented by morphological analysis alone should be borne in mind.

3.5 TAXONOMY OF EXTANT SPECIES

3.5.1 *MICROTUS AGRESTIS* (LINNAEUS 1761)

TAXONOMY

1761 *Mus agrestis* (Linnaeus)

1761 *Microtus arvalis agrestis* (Linnaeus)

1766 *Mus gregarius* (Linnaeus)

1792 *Mus arvalis nagricans* (Kerr)

1820 *Lemmus arvalis* (Nilsson)

1841 *Arvicola agrestis* (de Selys-Longchamps)

1844 *Lemmus insularis* (Nilsson)

1846 *Arvicola agrestis* (Owen)

1847 *Hypudaeus bucklandii* (Giebel)

1857 *Arvicola Agrestis* (Blasius)

1884 *Microtus agrestis* (Lataste)

1894 *Microtus (= Arvicola)* agrestis (Newton)

1896 *Microtus agrestis* (Barrett-Hamilton)

1910 *Microtus agrestis neglectus* (Hinton)

1910 *Microtus agrestis* (Trouessart)

1910 *Microtus agrestiodes* (Hinton)

DISTRIBUTION

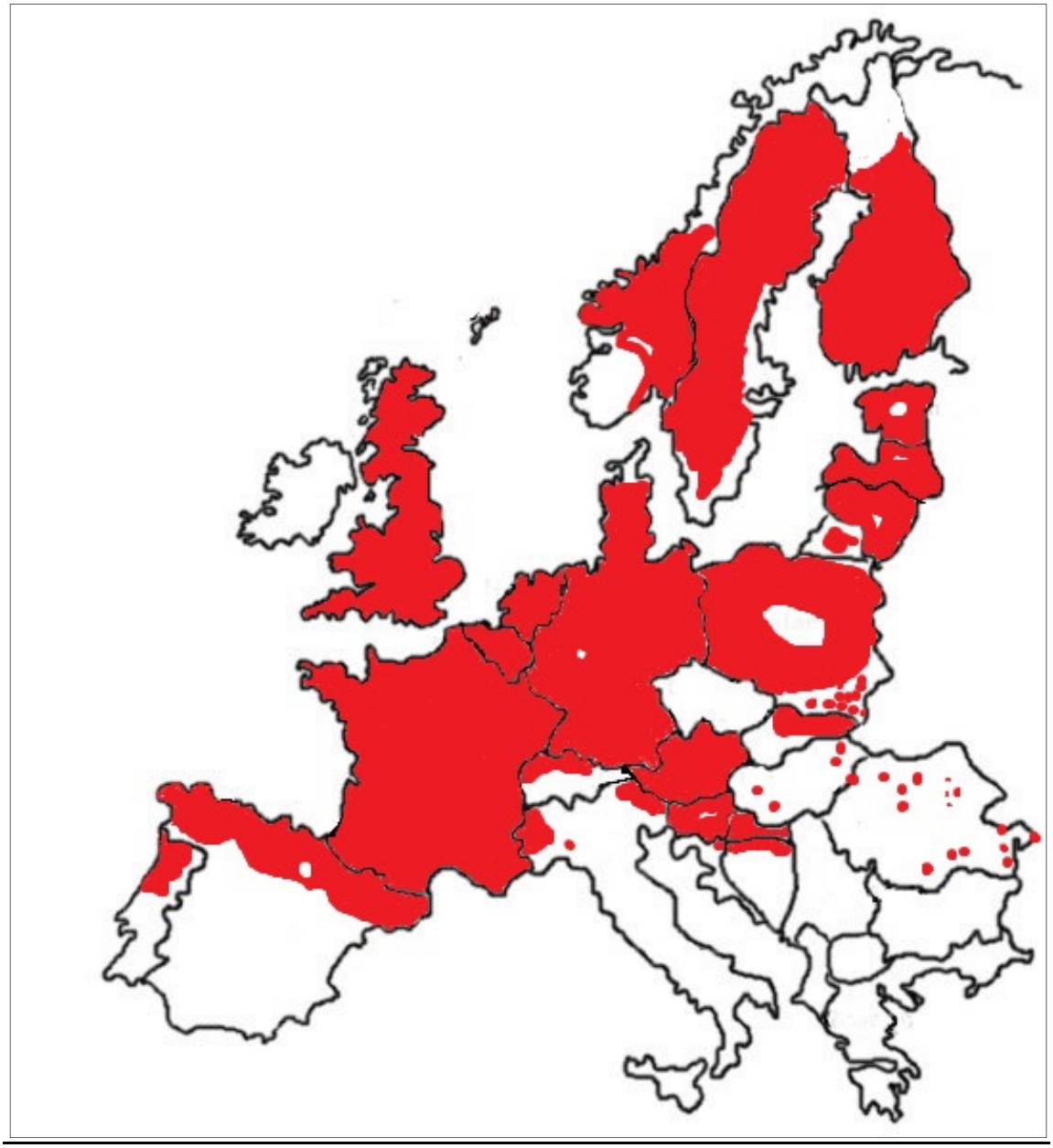

Figure 3.6: *Modern distribution of M. agrestis. Shaded areas denote presence (Modified from information in Amori, 1996a).*

M. agrestis, the short-tailed field vole, is the only species of *Microtus* found on the British mainland at the present day (Berry and Rose, 1975). M. agrestis currently inhabits the greater part of Europe, with the exception of areas exceeding 1,850m above sea level, southern Spain, Italy and many of the Balkan countries (Figure 3. 6).

HABITAT

M. agrestis inhabits moist, open environments including floodplain, shrub and rough grassland environments in a range of biotopes from montane and forested to tundra (Gromov & Polyakov, 1992). Although they dig burrows, they usually nest above ground (Musser & Carleton, 2005).

IDENTIFICATION

The earliest appearance of *M. agrestis* in the UK is reported to be in the early Middle Pleistocene Cromer Forest bed Formation (Norfolk/ Suffolk); however, this is based on an isolated M_1 (Hinton, 1926), which Hinton previously attributed to *M. nivalis* (Hinton, 1907). The first verifiable reports occur in the Hoxnian, at sites such as Hoxne (Schreve, 2000) and Clacton-on-Sea (Schreve, 2001).

The M_1 exhibits a very similar overlapping morphology to that of *M. arvalis* with a well developed T6 and T7 and five closed triangles (van Kolfschoten, 1991) (Figure 3.8). It is only possible to definitively differentiate the species from *M. arvalis* on the basis of the $M^{2,}$ as *M. agrestis* has an extra postero-lingual loop unlike *M. arvalis*.

It has also been suggested it is possible to differentiate the two species on the basis of the symmetry of the T4 and T5 regions in the M_1 and overall M_1 length (Nadachowski, 1984). However, this may be of limited use when comparing samples of different ages, due to increases and decreases in the overall size of the teeth and the relative sizes of dental areas in both species through time.

Living examples are relatively large, with their nose to tail length not exceeding 140mm. The skull is distinguished by the presence of an interorbital crest and the short and weakly curved lower incisor (Gromov & Polyakov, 1992; Figure 3. 7).

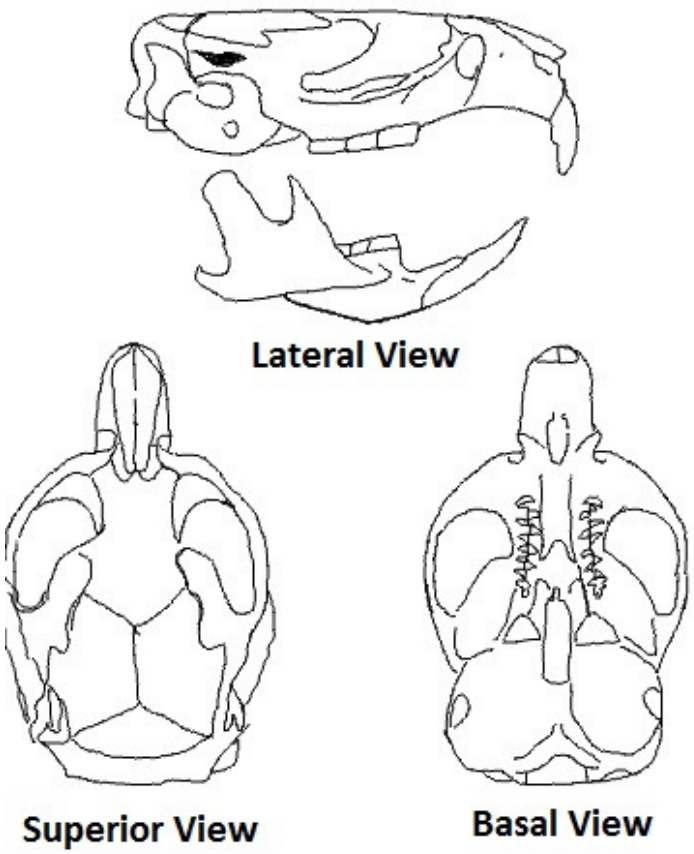

Figure 3.7: *Diagram of a generalised M. agrestis skull (modified from Miller, 1912).*

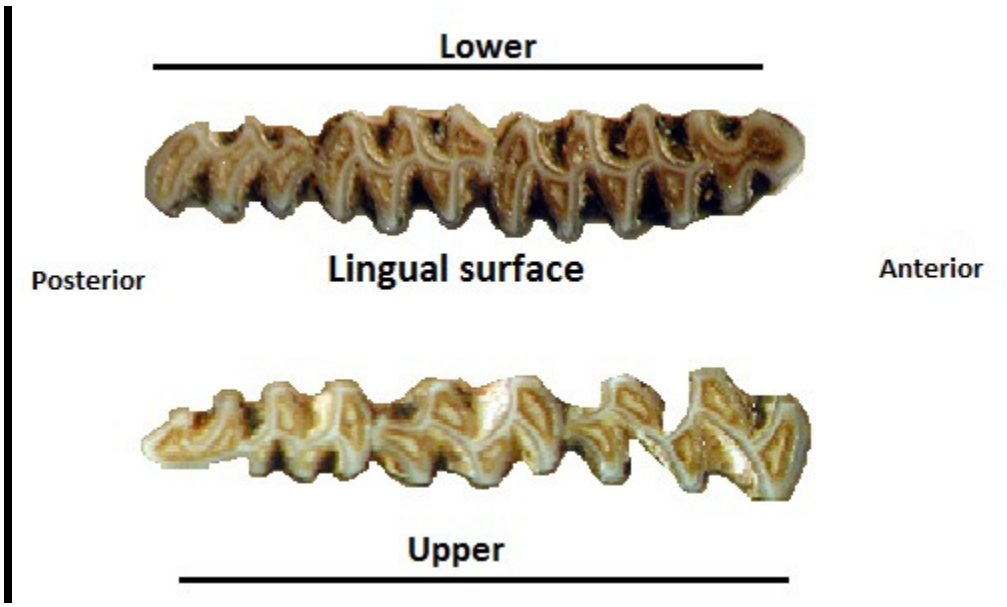

Figure 3.8: *Upper and Lower molar dentition of M. agrestis.*

3.5.2 *MICROTUS ARVALIS* (PALLAS, 1778)

TAXONOMY

1778 *Microtus arvalis* (Pallas)

1801 *Mus arvalis albus* (Bechstein)

1803 *Lemmus fulvis* (Geoffory)

1822 *Arvicola vulgaris* (Desmarest)

1840 *Arvicola arvenis* (Schinz)

1841 *Arvicola arvalis* (de Selys-Longchamps)

1845 *Arvicola arvalis* var. Ater (de Selys-Longchamps)

1847 *Arvicola cunicularis* (Ray)

1853 *Arvicola campestris* (Balsius)

1857 *Arvicola arvalis* (Blasius)

1884 *Microtus arvalis* (Lataste)

1905 *Arvicola arvalis galliardi* (Fatio)

1905 *Avricola arvalis forma variabilis* (Rörig, Börner)

1905 *Arvicola arvalis forma contigua* (Rörig, Börner)

1905 *Arvicola arvalis forma assimilis* (Rörig, Börner)

1905 *Arvicola arvalis forma depressa* (Rörig, Börner)

1905 *Arvicola arvalis forma simplex* (Rörig, Börner)

1905 *Arvicola arvalis forma principalis* (Rörig, Börner)

1910 *Microtus arvalis* (Trouessart)

1910 *Microtus arvalis* campestris (Trouessart)

1910 *Microtus corneri* (Hinton)

Up to thirty modern sub-species of *M*. *arvalis* have been identified (Gromov & Polyakov, 1992), based upon soft-tissue, skeletal elements, and DNA analysis. This highlights the huge range of variation within this species, which is likely to be reflected, at least in part, in the dentition.

DISTRIBUTION

In the UK, the common or Orkney vole, *M.arvalis*, is currently only present in the Orkney Isles off the eastern coast of Scotland, but is absent from the UK mainland. It is also absent from Scandinavia, all Mediterranean islands and the southern Balkan peninsula. (Figure 3.9) Elsewhere, *M. arvalis* is found up to 3000m above sea level (Von Krapp & Niethammer, 1982).

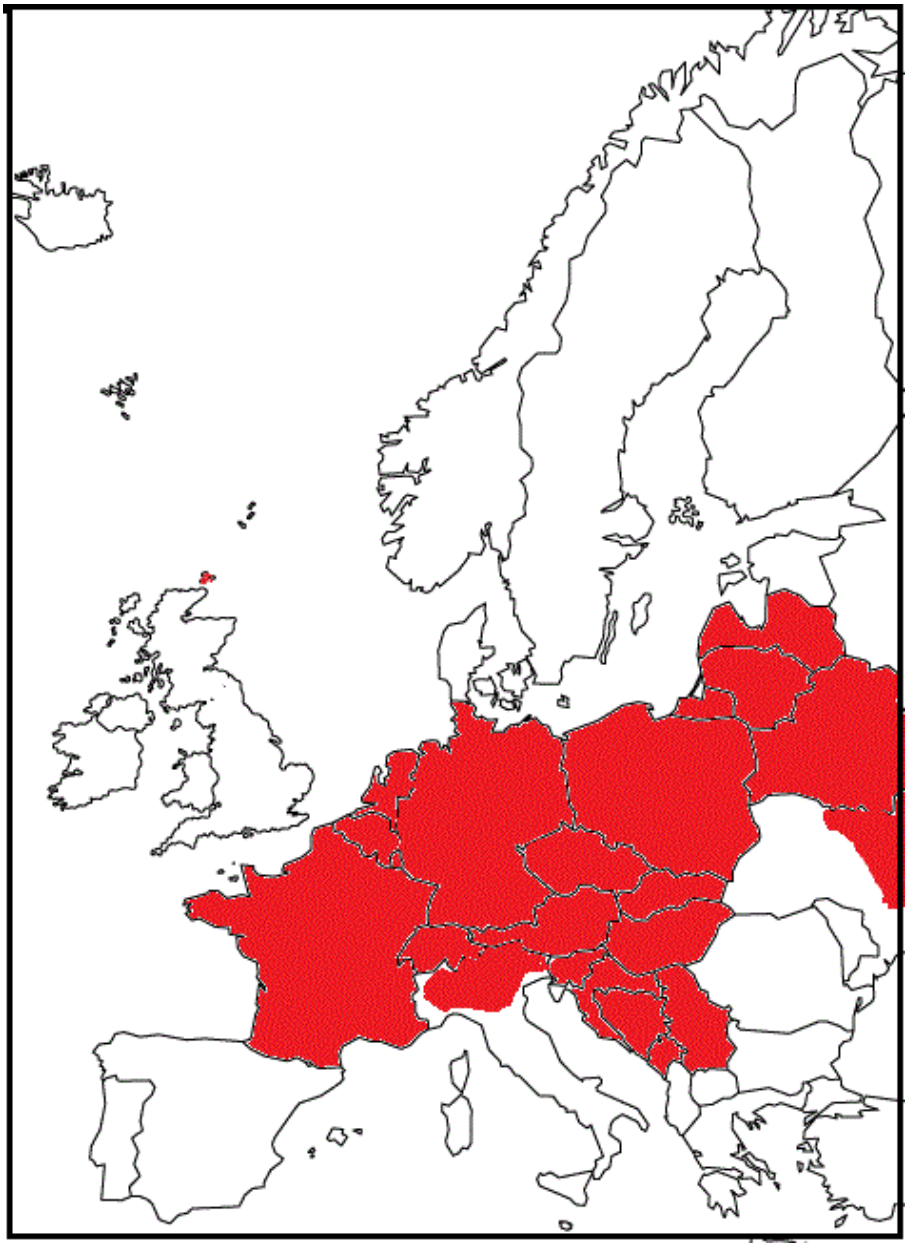

Figure 3.9: *Modern distribution of M. arvalis. Shaded areas denote presence (Modified from information in Amori, 1996).*

HABITAT

M.arvalis is found mainly within open meadow steppic environments and also cultivated areas in the present day, preferring little or no tree and shrub cover, including deforested areas. Its typical habitat is short, dry grassland and at the present day, it is most commonly found in grazed areas (Gromov & Polyakov, 1992).

IDENTIFICATION

The problems of separating *M.arvalis* and *M. agrestis* have led to a complicated and unreliable history of both species. One of the earliest sites at which *M. arvalis* has been unequivocally identified is that of Boxgrove, West Sussex, where both *M.arvalis* and *M. agrestis* are identified on the basis of size difference (Roberts & Parfitt, 1999). Distinguishing morphological features of the M_1 are the same as those given in the description for *M. agrestis* (Figure 3.11), with the major distinguishing feature between the two species being in the absence of an extra prostero-lingual loop on the M^2, as seen in *M. agrestis*.

An extinct species, *Microtus arvalinus*, was identified by Hinton (1923) on the basis of the distinctive morphology of the AC region, where the enamel surrounding T8 narrows and begins to separate T8 from the rest of the anteroconid complex. Modern *M. arvalis* is thought to be a descendent of this archaic type. It has the same morphology as *M. arvalis* / *agrestis,* but is smaller in size. Therefore, in this study, *M. arvalinus* will be considered a synonym of *M. arvalis*, as suggested by Chaline (1972), rather than a separate species (*contra* Hinton, 1923; Sutcliffe and Kowalski, 1976).

M. *arvalis* is a relatively small member of the genus, with larger examples not exceeding 100mm in length. The skull is highly variable, varying from convex to flat in dorsal profile (Figure 3. 10). The incisors are long, but display less curvature than other *Microtus* species (Gromov & Polyakov, 1992).

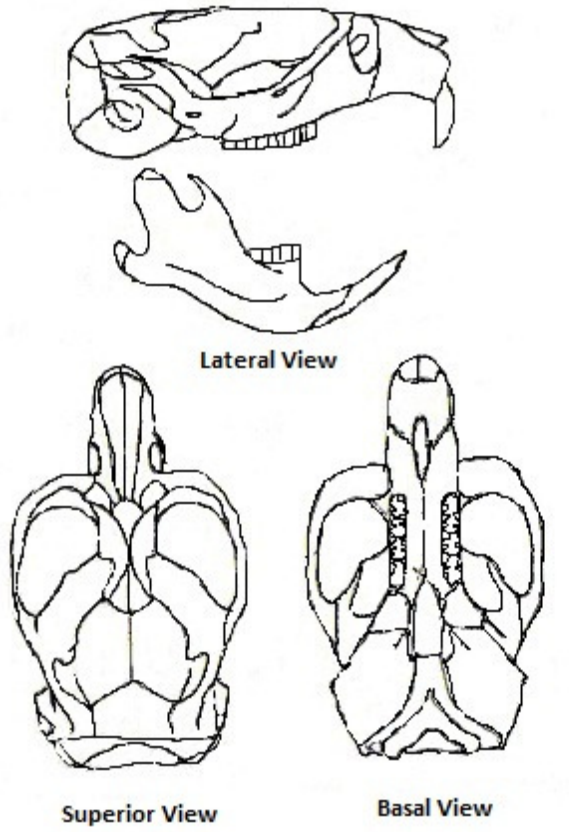

Figure 3.10: *Diagram of a generalised M. arvalis skull (modified from Miller, 1912).*

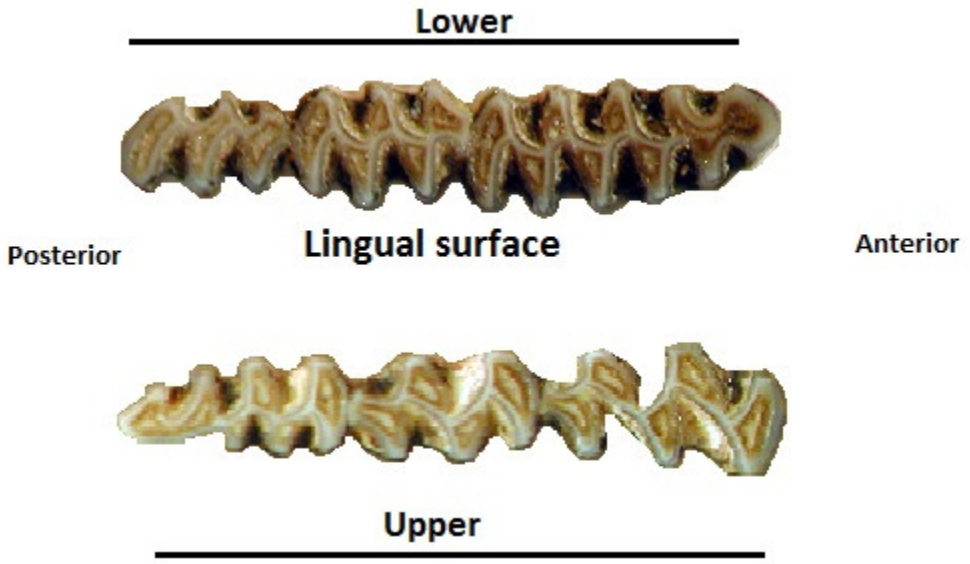

Figure 3.11: *Upper and lower molar dentition of M. arvalis.*

3.5.3 *MICROTUS GREGALIS* (PALLAS, 1779)

TAXONOMY

1779 *Microtus gregalis* (Pallas)

1894 *Microtus (= Arvicola) gregalis* (Newton)

1910 *Microtus anglicus* (Hinton)

DISTRIBUTION

M. *gregalis* is only found in Russia, China and Mongolia at the present day. It is absent from the UK and mainland Europe, although it was present throughout large areas of Europe during the Pleistocene (Figure 3.12).

HABITAT

The species is mainly found in wooded steppic and tundra environments (Von Krapp & Niethammer, 1982).

Figure 3.12: *Modern distribution of M. gregalis in Europe. Shaded areas denote presence (Modified from Baillie, 1996**).***

IDENTIFICATION

The modern species is mid-sized, with large individuals measuring up to 140mm in length, but smaller individuals reaching only 115mm. The skull is irregular in dorsal

profile, with highly curved incisors. The lower incisor does not extend beyond the margins of the dental foramen (Gromov & Polyakov, 1992; Figure 3. 13).

The narrow-skulled vole is easily identifiable using the $M_{1,}$ which displays T1-T5 closed triangles and a distinctive 'mitten shaped' anterior loop *(*Figure 3.14*).* The ancestral form, *Pitymys gregaloides* (Hinton, 1923), which evolved from the *Allophaiomys-Pitymys* lineage (Chaline, 1972), is first found in the UK in early Middle Pleistocene Cromerian Complex deposits at Westbury-sub-Mendip (Somerset) (Andrews et al., 1999) and West Runton (Norfolk) (Stuart, 1992) and is described below. The more derived form, *M*. *gregalis*, is found largely within the last cold stage (Devensian glaciation).

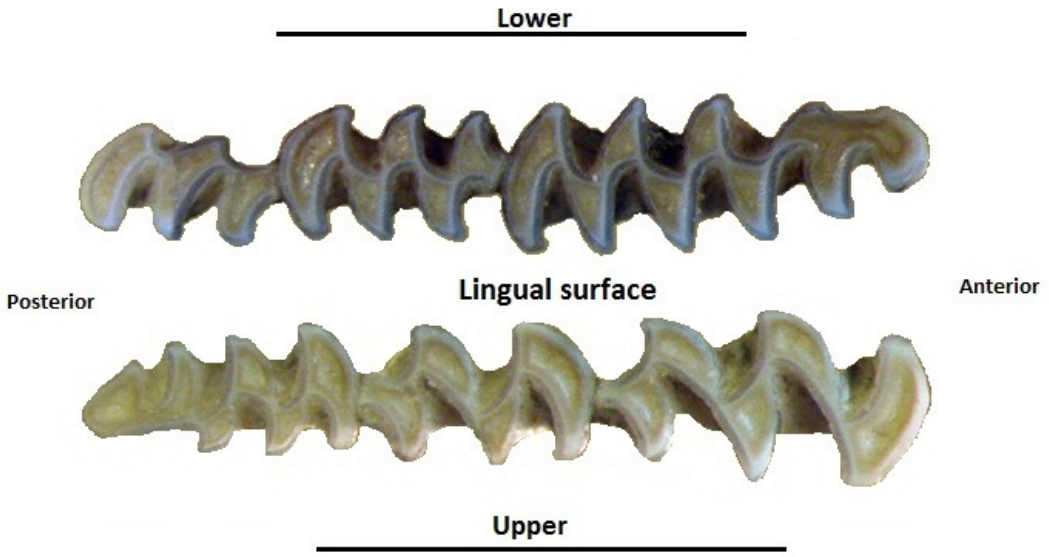

Figure 3.13: *Upper and lower molar dentition of M. gregalis.*

3.5.4 *MICROTUS (TERRICOLA) SUBTERRANEUS*

TAXONOMY

1836 *Pitymys subterraneus (de Selys-Longchamps)*

1845 *Hypudaeus rufescente-fuscus* (Schinz)

1845 *Hypudaeus rufofuscus* (Schinz)

1857 *Arvicola subterraneus* (Blasius)

1900 *Arvicola agrestis fusca* (Fatio)

1907 *Pitymys subterraneus* (Mottaz)

1910 *Pitymys subterraneus* (Troussart)

DISTRIBUTION

The modern *M*. *subterraneus* is solely a central and southern European species (Figure 3.14).

HABITAT

M. subterraneus is mainly found in open woodland and grassland, though it is capable of inhabiting a far wider range of habitats. It is found up to 1,700m above sea level (Gromov & Polyakov, 1992).

IDENTIFICATION

The pine vole has a complex history, with Hinton (1923) originally recognising two species of *Pitymys*, *P.gregaloides* and *P. arvaloides* within the early Middle Pleistocene Freshwater bed at West Runton (Norfolk), based upon the widely-confluent T4 and T5 molar triangles (the so-called "Pitymoid" structure) and the highly variable anterior loop, that are considered to be distinguishing features of the *Pitymys* lineage (for further discussion of the role of *Pitymys*, see below). It has since been recognised *that P. gregaloides* is likely to be the ancestral form of *M. gregalis* (Currant, 1986). However, *P. arvaloides* is also a synonym of the modern day *M. subterraneus,* and can be identified on the basis of several morphological features present in the M_1; T1-T3 are closed, with T4-T5 separated from the AC2 and displaying 'Pitymoid' characteristics, , and well-developed salient angles on the AC (Figure 3.19). No dental cement is present. It is also generally smaller in size than other *Microtus* species (Gromov & Polyakov, 1992).

The presence of *M*. *subterraneus* at a site can act as an important biostratigraphical marker. The LAD (Last Appearance Datum) for the species in the UK is in the Swanscombe Mammal-Assemblage-Zone (MAZ) dating to MIS 11, meaning that sediments containing *M. subterraneus* must date to 40,000 Kya or older (Schreve, 2001).

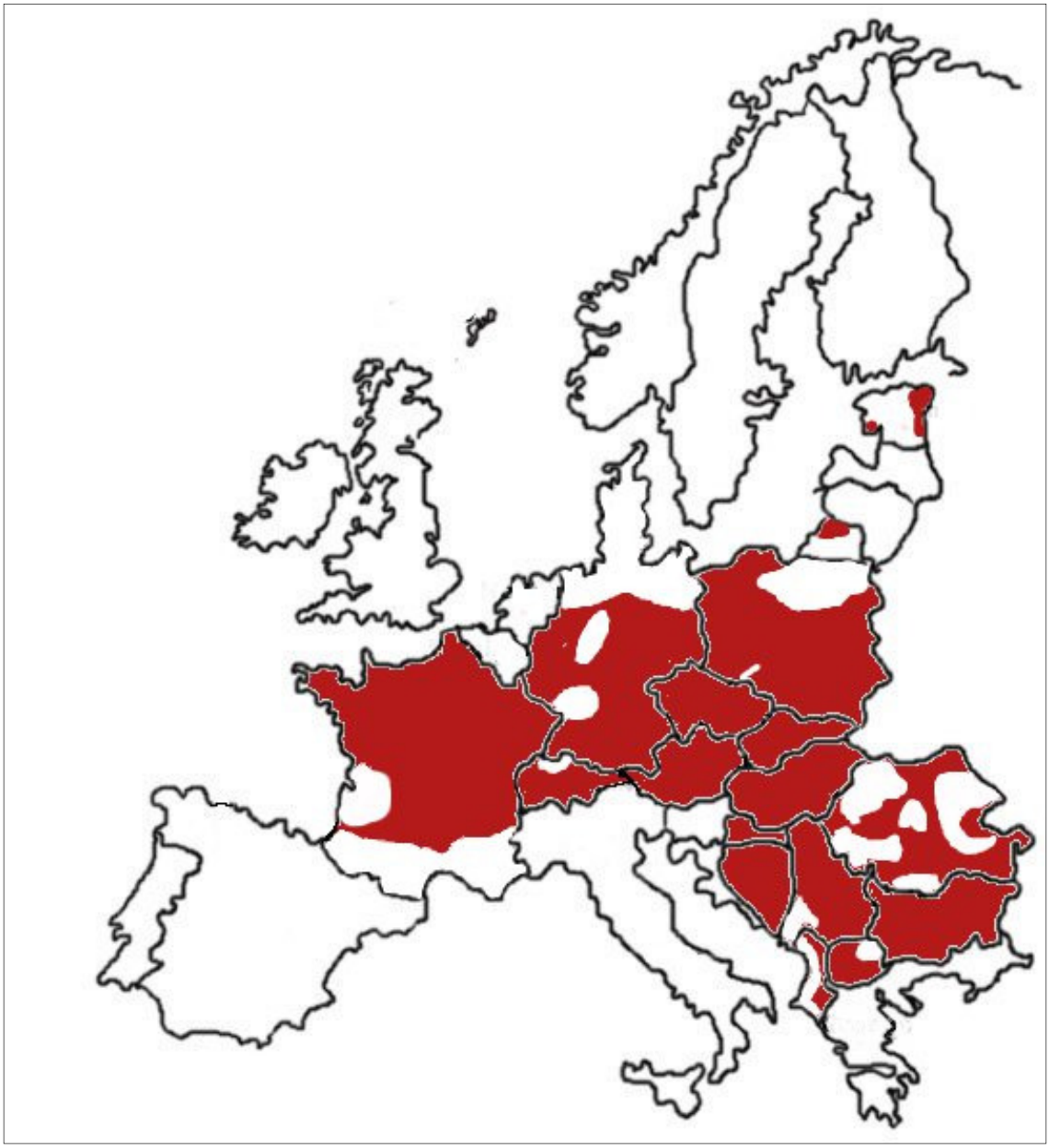

Figure 3.14: *Distribution map of M. subterraneus. Shaded areas denote presence (Modified from information in Amori, 1996**).***

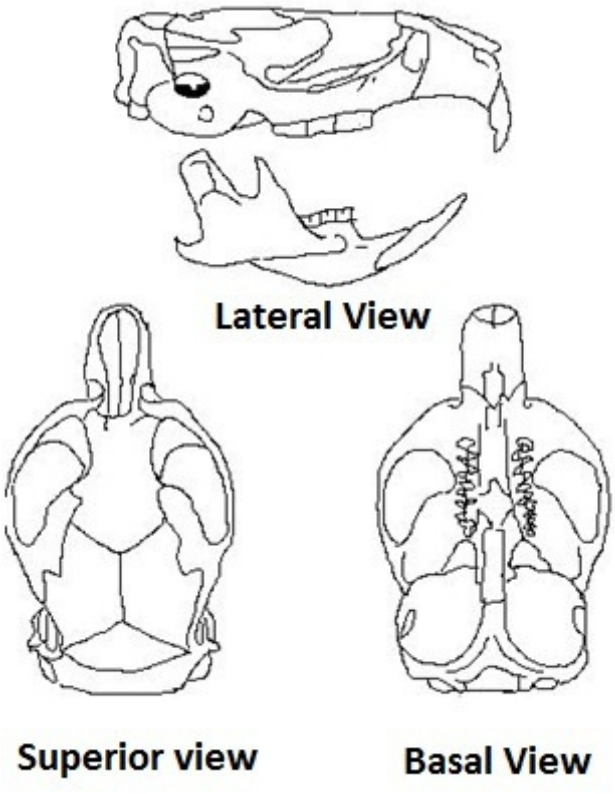

Figure 3.15: *Diagram of a generalised M. subterraneus skull (modified from Miller, 1912).*

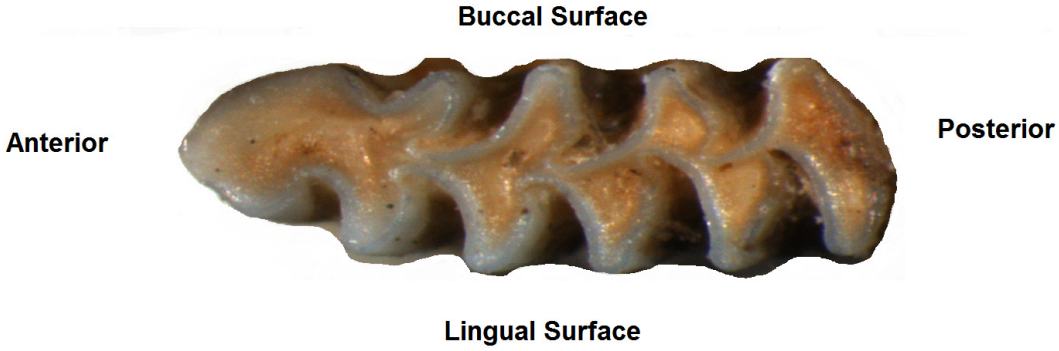

Figure 3.16: *M. subterraneus lower M_1.*

3.6 TAXONOMY OF EXTINCT SPECIES

3.6.1 INTRODUCTION TO PITYMYS

P. *pinetorum*, regarded as the type-species of *Pitymys*, is found in North America up to the present day and displays the 'Pitymoid structure', that is, T4 and T5 are broadly confluent (See figures 3.17, 3.18). Many species found outside North America also display this feature and have therefore been included within the *Pitymys* genus (Garapich & Nadachowski, 1996). However, much discussion as to the position of *Pitymys* as a separate sub-genus or a part of the evolutionary continuum between *Allophaiomys* and *Microtus* is present within in the literature, as discussed below. Modern examples of *Pitymys* display a similar dental morphology to *Microtus*, and may be indistinguishable morphologically (Nadachowski & Garapich, 1998). Some authors, such as Chaline (1972) have suggested that fossil *Pitymys* are morphotypes of *Allophaiomys pliocaenicus*, while others, such as Sutcliffe & Kowlaski (1976), suggested that Pleistocene remains of *Pitymys* represent 'true *Pitymys*' species. Brunet-Lecomte & Chaline (1992) argued that the Palaearctic and Nearctic members assigned to *Pitymys* do not share a common ancestor, and therefore, cannot be placed within the same genus. They suggest '*Terricola*' to replace *Pitymys* as the genus name for the Nearctic specimens. However, this suggestion is countered by Krystufek *et al*. (1996), who argued that the only real feature tying all the "Pitymoid" species together is the presence of the Pitymoid structure. These authors therefore declared the use of both *Terricola* and *Pitymys* invalid, as there is not sufficient evidence to group all species with the Pitymoid structure in a single genus under a common ancestor. On the basis of this evidence, they recommend that species previously assigned to *Pitymys* should

be regarded as a sub-species of *Microtus*. Markova & Maul (2007) proposed that 'Pitymoid' features are a morphological stage through which all species of *Microtus* had to pass during their evolutionary sequence.

For the purposes of this study, to avoid confusion with previously published accounts referring to *Pitymys* spp, *P*. *arvaloides, P*. *gregaloides* and *P*. *subterraneus* (e.g. Andrews *et al*., 1999, Roberts and Parfitt, 1996), the preferred nomenclature will be *Microtus* for all species which have previously been included within the umbrella of '*Pitymys*' species, with the understanding that the name '*Pitymys*' is not referring to a separate species or sub-species but rather to a set of characteristic morphologies within the genus *Microtus*. *P. gregalodies* will retain the *Pitymys* nomenclature as it is an important biostratigraphic marker, as discussed in chapter 1.

3.6.2 PITYMYS ARVALOIDES (HINTON, 1923)

1882 *Arvicola arvalis* Pallas (Newton)

1901 *Microtus (Pitymys) spp* (Major)

1923 *Pitymys arvaloides* (Hinton)

1958 *Microtus (Pitymys) arvaladiens* (Kretzoi)

1972 Allophaiomys *pliocaenicus* (Chaline)

Hinton (1923) identified *P. Arvaloides* on the general 'Pitymoid' M_1 characteristics outlined above, with the anterior loop resembling that of *M*. *arvalis* (Figure 3.17). He recorded the presence of *P. Arvaloides* in the Cromer Forest bed Formation. *P.*

arvaloides is thought to be a synonym of the modern day *M. subterraneus* (Schreve, 1997). The presence of M. *subterraneus* with 'Pitymoid' morphology has been identified in the UK from the Cromerian to the Hoxnian periods (Sutcliffe & Kowalski 1976).

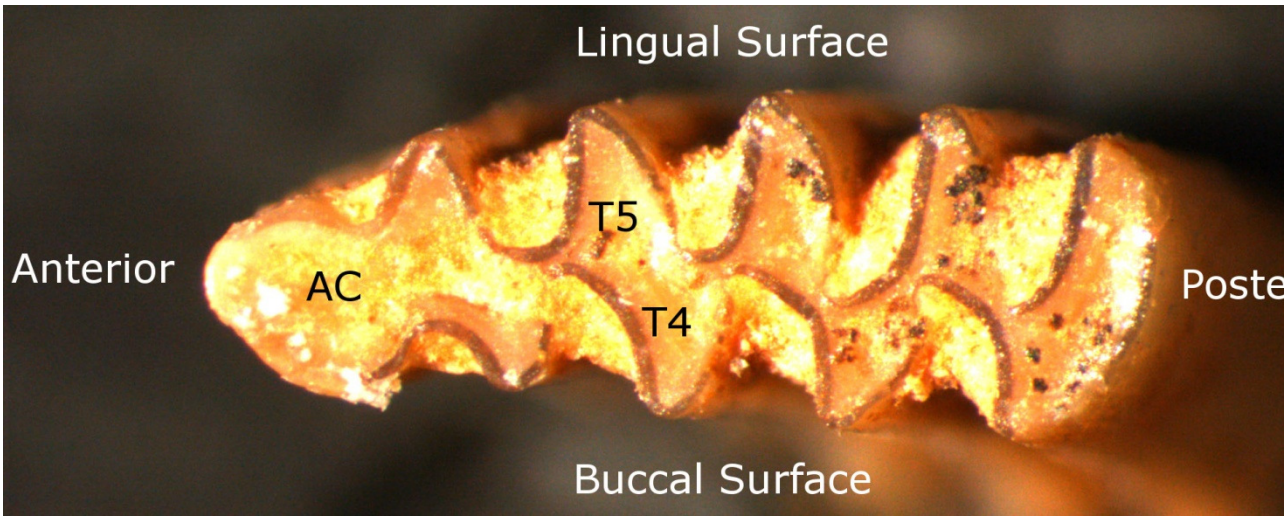

Figure 3.17: *P. arvaloides lower M_1 (modified from Hinton, 1923). T4 and T5 can be seen to be approximately parallel, in comparison to other Microtus species where they are divergent (see figure 3.5 for generalised Microtus dentition showing T4 and T5 clearly separated)*

3.6.3 PITYMYS GREGALOIDES (HINTON, 1923)

1882 *Arvicola gregalis* (Newton)

1891 *Microtus (Arvicola) gregalis* (Newton)

1923 *Pitymys gregaloides* (Hinton)

1972 *Allophaiomys pliocaenicus* (Chaline)

Pitymys gregaloides is a relatively rare component of British Pleistocene mammalian assemblages but is extremely common at the early Middle Pleistocene site of Westbury- sub-Mendip, (Andrews et al., 1999) and is also identified at West Runton (Stuart, 1992). The species is not known in the UK after the Anglian glaciation *(*Sutcliffe & Kowalski, 1976).

P. *gregaloides* is the suggested ancestor of *M*. *gregalis* (Chaline, 1972), and Hinton (1923) identified the species on the basis of the general M_1 *Pitymys* characteristics outlined above, with the addition of the presence of an anterior loop resembling that of *M*. *gregalis* in form.(Figure 3.18).

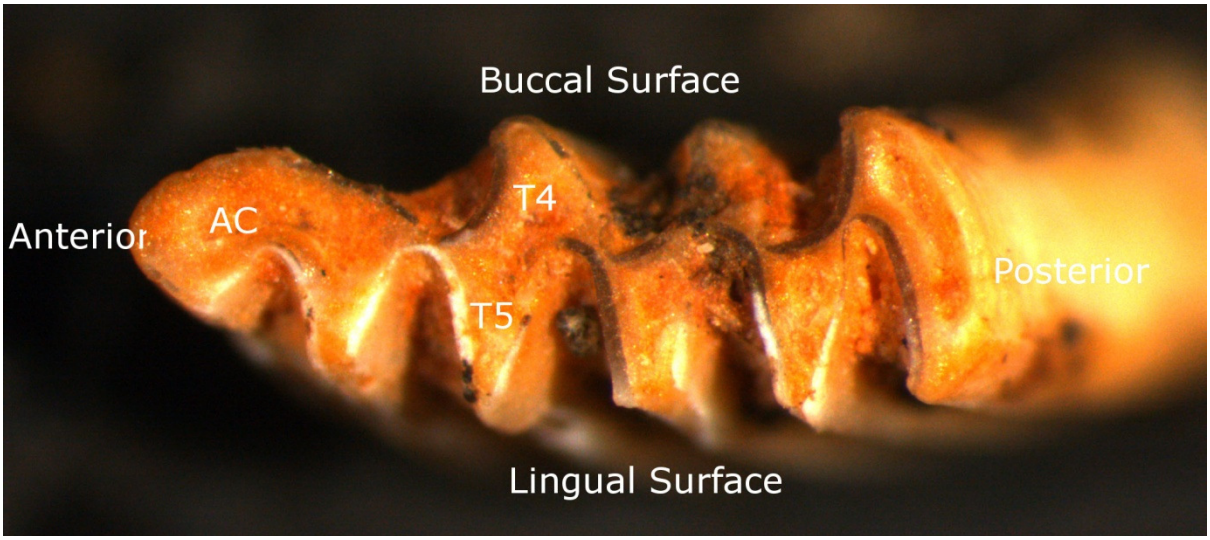

Figure 3.18*: P. gregaloides lower M_1 (Hinton, 1923). T4 and T5 can be seen to be approximately parallel, in comparison to other Microtus species where they are divergent (see figure 3.5 for generalised Microtus dentition showing T4 and T5 clearly separated)*

CHAPTER 4
MATERIALS AND METHODS

4.1 MATERIALS

This study is based upon data from a sample of lower first molars (M_1) from 1435 specimens, including 1051 specimens from 5 archaeological sites and 384 from 24 modern locations (Table 4.1; more detailed information about specimen location can be seen in figures 4.1, 5.1 ,6.1 and 7.1 for Modern, Walou, Boxgrove and Westbury samples respectively). Lower first molars are most frequently preserved intact in archaeological and palaeontological samples (Andrews, 1990) and are therefore the teeth which are most frequently analysed in the literature.

	Modern	Walou	Boxgrove	Westbury	Cudmore Grove	West Runton
M. arvalis	96	0	0	0	0	0
M. agrestis	72	0	0	0	19	25
M. arvalis/ agrestis	0	165	91	217	0	0
M. gregalis	98	18	4	0	0	0
M. subterraneus	118	0	41	0	0	0
P. gregalodies	0	0	0	352	0	0
P. arvalodies	0	0	0	119	0	0

Table 4.1: *Species composition of all samples within this study.*

Due to variability in sample numbers between sites and/or stratigraphic levels, the maximum number of individuals sampled per species in each sample/level is set at 50, in order to provide large representative samples, while at the same time keeping the sample sizes equal where possible. Where 50 individuals are not available, all

individuals within the sample are recorded. The smallest acceptable sample size is set at 5 individuals/ 10 teeth. For each sample, the provenance, unique sample number, location and side are recorded.

Only adult individuals are included within the sample, as determined by consistent wear across the whole surface of the tooth. Both left and right teeth are included in the samples. Any teeth which display damage within areas of landmark placement are excluded from sampling. In modern samples, the sex of the individual is recorded. However, in archaeological samples it is not possible to determine the sex of each individual from the dental remains. Therefore, mixed sex samples, possibly containing left and right hand side teeth from the same individual, are used throughout the analyses. To test the validity of using mixed samples, analyses are undertaken on modern samples where both sex and side of teeth are known (see chapter 4 for details). Results show that sex does not have a significant effect upon the morphology or size of the teeth (Table 4.2). Polly et al.,(2011) have shown there can be a significant amount of random shape asymmetry between the left and right side teeth of the same individual in *Microtus* species. Individual teeth are frequently shown to be morphologically more similar to those from other individuals than to the corresponding tooth from the other side of the same individual. Therefore, if a sample contains both left and right hand teeth, this should not introduce duplication of information, but rather allow the analyses to sample the full variability of lower M1 morphology within each sample population.

All modern specimens used in the study are held at the department of Zoology at the Natural History Museum, London. Walou cave specimens are held by Dr John Stuart at the University of Bournemouth and Westbury and Boxgrove specimens are held in the

department of Palaeontology, Natural History Museum, London. All modern specimens are teeth in undamaged mandibles, mostly with attached skulls collected from live specimens, and therefore preservation is excellent. In all three archaeological samples, intact mandibles are extremely rare, and samples largely consist of individual loose teeth. Walou cave and Boxgrove samples are both taken from samples collected via fine-mesh sieving of bulk sediments (Parfitt, 1999; Stuart, J, pers. comms), in which many M_1 teeth are incomplete, possibly as a result of sieving damage and taphanomic damage due to predation etc. (Andrews, 1990). At Westbury sub-Mendip, the samples were recovered from sediments via a combination of acid erosion of Breccial sediments, sieving and hand-picking. Specimens tend to exhibit less taphonomic damage to teeth than displayed at Walou or Boxgrove; however this could be an artefact of choosing the best specimens from the extremely abundant samples at this site. Incomplete or damaged M_1 teeth are excluded from analyses, reducing the sample sizes dramatically from the number of identifiable teeth available.

4.2 METHODS OF DATA COLLECTION

Several different methods of data acquisition and analysis are performed in this study, and are described below.

4.2.1 DATA ACQUISITION

Data are in the form of two-dimensional landmarks (biologically homologous points- see section 4.2.2 for detailed explanation), digitised from photographs of the occlusal surface of the M_1. Each specimen was photographed using a Leica DFC295 camera

attached to a binocular microscope. Landmarks are digitised from specimen photographs using a Wacom Intuos 2 A5 digitizing tablet in tpsDig.

4.2.2 LANDMARK DATA

Morphological variation in *Microtus* molars are best described using two dimensional analyses of the occlusal surface of the M_1, as the occlusal surface does not contain protuberances or cusps and the teeth are permanently growing , therefore the shape of adult teeth should not vary with wear or age (Gutherie, 1965). Landmarks are biologically homologous points; i.e. precise areas of a biological structure which can be located upon every specimen within a dataset. Therefore, the selection of suitable landmarks to represent a complex biological shape such as *Microtus* teeth is extremely important.

Bookstein (1991) identified three categories of landmarks, based both on their perceived accuracy in defining homologous points and the type of information which can be derived from them. Type 1 landmarks are the optimal landmark form, and landmarks of this type are placed in areas with strongly defined boundaries, such as the suture between two biological structures. Due to the fact that type 1 boundaries are surrounded in all directions, they allow the direction from which the forces or processes which are causing the movement of landmarks to be identified.

Type 2 landmarks, however, cannot provide this type of information, as they are situated on areas which are defined by other structures, such as the tip of a bony process or the maxima/ minima of a curve.

Type 3 landmarks are at the extreme of what can be defined as a landmark, and are defined as having at least one deficient co-ordinate, and characterize more than one region of the form - Eg; the lowest point of a concavity.

The homologous landmarks used in this study and their landmark types are shown in table 4.2 and figure 4.1. The fixed landmarks (1-15) are type 2 landmarks, as they are placed on the maximum or minimum curvature of each triangular structure. All sliding semi-landmarks (16-25) are type 3. Due to the curved nature of *Microtus* teeth, it is not considered possible to place type one landmarks accurately.

4.2.3 SLIDING SEMI-LANDMARKS

The region of the *Microtus* M_1 thought to contain the largest amount of morphometric variation is the AC region (Gutherie, 1965).However, due to the curved nature of this area, the placing of traditional, homologous landmarks is not possible (see figure 3.5 for generalised *Microtus* tooth diagram and named areas), as no such landmarks can be identified on this part of the tooth outline. Therefore, in order to capture the maximum amount of shape variation within the *Microtus* teeth, sliding semi-landmarks are placed in this region (landmarks 15-25, fig 4.1.) and combined with the standard landmarks on each triangle.

Two possible methods of placing semi-landmarks exist, Minimum Bending Energy, whereby the landmark points are allowed to move within a parallel plain in order to minimise the amount of bending energy required to fit the landmark to the reference specimen (Green, 1996; Bookstein, 1997; Bookstein *et al.*, 2002) and Procrustes Distance whereby each of the landmarks are moved so that they lie along lines which are perpendicular to those of the same semi-landmark in the reference shape (Sampson *et al.*, 1996; Sheets *et al.*, 2004).

Sliding semi-landmarks function using a variation of Procrustes superimposition whereby the semi-landmark points are re-arranged along the outline curve until they match the position of the points on the reference specimen (the mean form as calculated in Generalised Procrustes' Analysis) as closely as possible. In this project, semi-landmarks are calculated using tpsRelWar, which utilises the Minimum bending energy method.

The archaeological samples contain seven species, of which six; *M. agrestis*, *M. arvalis*, *M. gregalis* and *M. subterraneus*, *P. arvaloides* and *P. gregalodies,* are similar enough in shape to allow the placement of equivalent homologous landmarks across species. These species are all included in the subsequent analyses.

M. oeconomus specimens are also present within the archaeological samples at all sites. However, due to the morphology of *M. oeconomus* being significantly different from the other species of *Microtus*, *M. oeconomus* is excluded from these analyses, as the placement of landmarks homologous with the other *Microtus* species is not possible.

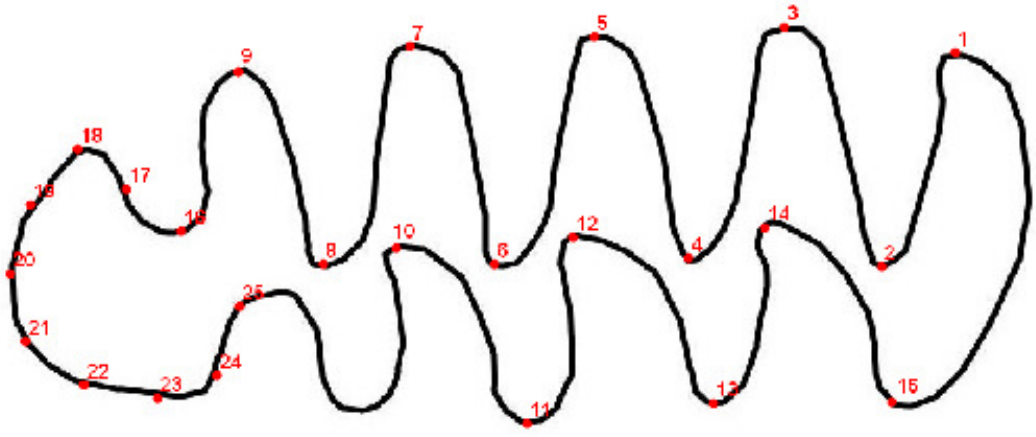

Figure 4.1: Standardised Microtus M_1 showing locations of type 2 homologous (1-15) and semi-sliding (16-25) landmarks.

LANDMARK	LOCATION
1	Point of maximum curvature of lingual salient angle 1
2	Point of maximum curvature at junction of LSA1 and LRA1
3	Point of maximum curvature of T1 at junction of LRA1 and LSA 2
4	Point of maximum curvature at junction of LSA2 and LRA2
5	Point of maximum curvature of T1 at junction of LRA2 and LSA 3
6	Point of maximum curvature at junction of LSA3 and LRA3
7	Point of maximum curvature of T1 at junction of LRA3 and LSA 4
8	Point of maximum curvature at junction of LSA4 and LRA4
9	Point of maximum curvature of T1 at junction of LRA4 and LSA 5
10	Point of maximum curvature at junction of BSA3 and BRA3
11	point of maximum curvature of T1 at junction of BRA3 and BSA2
12	Point of maximum curvature at junction of BSA3 and BRA2
13	point of maximum curvature of T1 at junction of BRA2 and BSA1
14	Point of maximum curvature at junction of BSA2 and BRA1
15	Midline of the point of maximum curvature of Buccal salient angle 1

Table 4.2: *Descriptions of locations of type 2 homologous landmarks on Microtus M_1 teeth (landmarks 1-15).*

4.3 METHODS OF DATA ANALYSIS

4.3.1 INTRODUCTION TO GEOMETRIC MORPHOMETRICS

As described in chapter 1, Geometric Morphometrics encompasses a suite of analytical methods which can be used to quantify the shape of biological organisms. In biological studies, shape is often used to separate and categorise organisms, either by looking at the live form or its skeletal elements. Shape can be a powerful tool when looking at variation caused by biomechanical, functional or environmental adaptations influenced by selective evolutionary pressures or factors related to taxonomy, ontogeny and growth (Bookstein, 1991).

Geometric Morphometric (GMM) analyses were originally devised in an attempt to address the limitations of standard morphological analyses and GMM now represents an alternative to traditional, standard morphometric methods which allows the full shape of a biological organism or element to be studied, independently of size. Because the shape as a whole is analysed, this also means that it is possible to identify the areas of the organism or element which are different, how they change in relation to one another and for these differences to be graphically represented easily, through the use of multivariate statistics (Bookstein, 1991).

Geometric morphometric analysis also represent an advantage over traditional morphometric methods as the geometrical aspect of the data is preserved through all analyses, allowing the areas of an organism in which shape change occurs to be identified, along with the amount of variation present (Slice *et al.*, 1996). Geometric

morphometric analysis also allows graphical representations of shape and shape change to be created.

Therefore, due to the advantages of GMM over standard qualitative and quantitative analyses, GMM methods are selected for use in this study and are described in detail below.

All analyses in this study are executed in *MorphoJ* (Klingenberg, 2008) unless otherwise noted.

4.3.2 GENERALISED PROCRUSTES ANALYSIS

Morphometric analysis requires that factors such as translation, rotation and size are removed from the data set, leaving only data which directly describes the shape of the samples, and allowing shape to be analysed independently of size.

Generalised Procrustes Analysis (GPA) is a method of isolating shape data from these factors. GPA aligns all specimens to a randomly chosen reference specimen within the dataset, removing non-shape- dependent differences between specimens by rotating, translating, reflecting and scaling forms to the reference specimen by minimising the sum of squared distances between homologous landmarks. All specimens are then scaled according to the square route of the sum of squared distances of all landmarks to the mean of all landmarks for the shape of the object, known as the centroid (Gower, 1971; Rohlf and Slice, 1990). The resulting scaling factor is known as centroid size, which is the only scaling variable which does not introduce bias to the analysis as it is uncorrelated with the shape of an organism, in the absence of an allometric

component to the dataset. Therefore, it allows size and shape measures to be easily separated in analyses (Bookstein, 1991).In GPA, equal weighting is given to all landmarks and therefore, less bias towards specific regions of the morphology is introduced (O'Higgins *et al.*, 2001). Therefore, if variation within the sample is small, the variation from the reference shape will be small (Kent, 1994). The size of individuals may be of interest when investigating questions such as ontogenetic change and can be added to shape data as a variable in analyses, for example, in Procrustes form space, where Procrustes co-ordinates are plotted against size within the analyses.

4.3.3 MULTIVARIATE REGRESSION

In multivariate regression, several dependent variables are plotted against an independent variable. In the case of this study, multivariate regression is used in order to calculate the allometric effect within the dataset.

The centroid size of each individual, as calculated during GPA, is plotted against Procrustes fitted co-ordinates and the vector of regression coefficients is formed by the covariances of each shape variable and size, divided by the variance of size (Timm, 2002).

4.3.4 KENDALL'S SHAPE SPACE

Kendall's shape space (Kendall, 1984) is the space in which each individual data point is represented after GPA registration. Kendall's shape space consists of

km-m – (m-1 /2) -1 dimensions

Where k= the number of landmarks and m= the dimensionality of the landmarks. In analyses using large numbers of landmarks, Kendall's shape space becomes highly complex due to the high number of dimensions and the non-Euclidean nature of the shape-space, meaning that statistical analysis of data within Kendall's shape space is highly complex and must be approached with caution. The non-Euclidean (i.e. curved) nature of the shape-space could cause distortion in the analyses of data using standard statistical techniques for Euclidean spaces. However, it has been estimated that the amount of variability is small enough that the data only occupies a small section of all the potential configurations of the number of landmarks used. Therefore it is possible to project the data points from Kendall's shape space onto a linear tangent space within which further statistical analyses take place (Dryden and Mardia, 1998). Slice (2001) notes that Procrustes scaling to the sample mean configuration of landmarks provides the best method within Kendall's shape space, in as it minimises distortion as a result of multi-dimensional data being projected into tangent space, as compared to projections from Kendall's shape space directly.

4.3.5 PRINCIPAL COMPONENTS ANALYSIS

Once Procrustes-aligned data are projected from Kendall's shape space into the linear tangent space, Principal Components Analysis (PCA) can be used to explore relationships within the data.

PCA is a method of summarising and analysing differences in shape, distribution of variance within a sample and highlighting similarities or differences between and

within groups of data. PCA analysis produces a point for each specimen in multidimensional space creating a multidimensional cloud of specimens. It calculates the principal axes of variation within this cloud known as Principal Components (PCs). As PCs are orthogonal to each other, the initial number of potentially correlated variables within a dataset is reduced to a smaller number of statistically independent variables (Palmer, 2004). This reduces the dimensionality of the data while retaining most of the original variability (Boersma and Weernik, 1999). Values for the amount of total variation within a sample represented by a PC are given as Eigenvalues. PC1 is the axis of variation that explains the largest amount of variation within the sample, PC2 the second, and so forth. The majority of variation within a sample will normally be explained by a relatively small number of Principal Components.

When a PCA is carried out, the point of intersection of all axes represents the mean shape of all the specimens included in the analysis after GPA.

4.3.6 PROCRUSTES FORM SPACE

Procrustes Form space is used within this study to investigate the relationship between size and shape within datasets. Landmark coordinates are Procrustes-fitted to remove the effects of scale, orientation and location. However, the scale of the specimens is reintroduced to the dataset using log centroid size (as calculated during Procrustes fitting), prior to carrying out PCA (Mitteroecker *et al.*, 2004). Procrustes form-space was calculated in PAST (Hammer *et al.*, 2001).

4.3.7 PROCRUSTES DISTANCES

Procrustes Distance is used to measure the degree of fit between individual specimens or the sample means in Kendall´s shape space, providing a measure of biological distance. It is measured as the square root of the sum of squared differences between Procrustes fitted landmarks.

4.3.8 MAHALANOBIS' DISTANCES

Mahalanobis' distance (D^2) is the squared distance between two means divided by the pooled sample variance-covariance matrices i.e.; the statistical distance between means of groups, relative to the variance within the groups. Therefore, D^2 is a measure of shape differences between groups within a sample, taking into account the covariance and variance within each group. D^2 differs from Procrustes distance as Procrustes distance measures the distance between specimens in Kendall's shape space, unlike D^2 measurements, which are a general statistical distance. In this study Mahalanobis' distances are used to assess the reliability of a set of predictors to predict group membership (Tabachink & Fidell, 2001).

4.3.9 DISCRIMINANT FUNCTION ANALYSIS

Discriminant Function Analysis (DFA) is used to determine which continuous variables, if any, discriminate between two or more naturally-occurring known groups. In a DFA, it is assumed that all groups represent a sample from a normally-distributed group.

The independent variables are the predictor variables and the known groups are the dependent variables. A total variance/co-variance matrix is calculated alongside a matrix of pooled within group variance/co-variance, based upon Mahalanobis distances between groups. The two matrices are compared using multivariate F-tests to determine whether there are any significant differences between pairs of groups. Discriminant functions between each pair of groups are orthogonal. If discriminant functions between groups are shown to be statistically significant, groups can be distinguished based upon predictor variables. Unknown specimens can then be assigned to known groups based upon predictor variables of the known groups (Timm, 2002).

Discriminant function analysis can be used to assign unknown individuals to a group using known data. Group membership is predicted from a set of variables according to difference in Malahanobis´ D^2 between group means. Therefore, the smaller the Malahanobis distance of the individual to the group centroid, the more likely it is that the individual belongs to the group (Tabachnick & Fidell, 2001).

4.3.10 CROSS-VALIDATION

Cross-validation is used to assess the reliability of classifications made in Discriminant Function analysis. The leave-one- out method of cross validation removes a specimen of a known group at random from a dataset and re-calculates the discriminant function without the removed specimen. The removed specimen is then treated as a specimen of unknown grouping and reclassified to a group based upon the distance of its discriminant function from the group mean. This analysis is then repeated for each sample in turn, for a specified number of times (in the case of these analyses, 1000

times). Results from cross-validation indicate how many times the known samples have been assigned to the correct group. If a high percentage of the samples have been assigned to the correct group, a high degree of confidence can be placed in samples of unknown grouping that are assigned to a group using discriminant analysis. All Cross-validation analyses are calculated using the R statistical analysis package (R Foundation for Statistical Computing, 2009).

4.3.11 STUDENT'S T-TEST

Student's t-test is a parametric test used to calculate whether 2 samples are significantly different from one another. In order to do this, the difference in means of two samples is calculated, assuming normal distribution in both populations. The resulting t-values are then converted into p-values via a conversion table.

T-tests are performed in Microsoft Excel (Microsoft Corporation, 2007).

4.3.12 ANALYSIS OF VARIANCE

In order to compare the variance within samples, variance within each group (eg; stratigraphic level/ climatic conditions etc) is calculated from the Procrustes fitted coordinates of all specimens within that group. A range of variance values is then calculated by bootstrapping the original data 1000 times. Bootstrapping is a resampling technique that randomly re-samples the dataset in order to gain an estimation of the sample distribution, and to assign measures of accuracy to sample

estimates (Efron & Tibshirani, 1994). The bootstrap values are then plotted to provide curves illustrating the distribution of variance in shape-space for each sample. All variance analyses are performed in Microsoft Excel (Microsoft Corporation, 2007).

4.4 VISUALISATION OF SHAPE CHANGES

When working with GMM data, it is important not only to quantify morphological differences between samples, but also to visualise them, particularly when trying to understand and describe changes with biological organisms. Methods of visualising data used in this study are described in the following subsections.

4.4.1 THIN PLATE SPLINES

Thin plate splines are a method of displaying shape change, allowing the relative movements of landmarks across a form to be easily visualised. The basis of a thin-plate spline is a flat Cartesian transformation grid, overlaid on a reference shape (such as the mean shape of all specimens within the analysis). The grid is then deformed to the target shape according to the minimum 'bending energy' required to transform the grid to fit the landmark points of a specimen exactly to the reference shape (Bookstein, 1989). The distortion of the grid provides useful visual analysis of areas of morphological variation within a shape, as well as the nature and magnitude of the variation. Thin Plate Splines within this study are created using Morphologika (O'Higgins & Jones, 2006).

This type of analysis is particularly useful when applied to a PCA diagram. Within a PCA, the mean shape of all specimens (0, 0 in PCA co-ordinates) is taken as the 'flat' Thin Plate Spline and then any point within the PCA can be selected and the mean shape is warped to the shape represented by the selected point. This is useful when trying to visualise tooth morphology as a change from the mean shape of the sample.

4.4.2 UPGMA

Dendrograms are used to represent relationships in shape observed within a sample. In this study dendrograms are calculated using the Un-weighted Pairgroup Method using Arithmetical averages (UPGMA) clustering method of producing phenographic trees. This creates a two dimensional representation of the multi-dimensional data in Kendall's shape space, depicting the relationships between the groups in a linear fashion. UPGMA calculates the average similarity or dissimilarity of each individual within the group to the whole group to which it is assigned. Each specimen is given equal weighting. The average of each group is then used to calculate a new distance matrix, which produces new distance measurements between the groups and can be used to produce a phenogram (Sneath and Sokal, 1973). All UPGMA trees are produced using NTSYS 2.11 (Applied Biostatistics inc. 2000).

4.5 MEASUREMENT ERROR

To ensure the reliability of the data collected within this study, two analyses of measurement error are performed, as described in the following subsections;

4.5.1 COLLECTION ERROR

In order to ensure accuracy and reduce errors within the datasets, care is taken to ensure that the occlusal tooth surface was directly parallel with the camera, with all areas of the surface equally in focus. A scale for each specimen is recorded using a graticule, under the same magnification as the corresponding specimen and then added to the specimen photograph using Adobe Photoshop 7.0 (1990-2002 Adobe Systems Incorporated). Additionally, photographs of 3 randomly selected specimens were taken 12 times each (4 times per day on 3 separate days, with the microscope reset between photographs). Measurements are then taken of the greatest length of the specimen in reference to the scale in TPSDig in order to assess the accuracy of the photographic technique (Table 3.2).

The standard deviation of the repeated results is 0.005149, 0.006216 and 0.006216 mm for specimens 1, 2 and 3 respectively. The variation between repeat measurements is thus very small, representing an average of 2% of the average tooth measurements, and likely to have been caused by human error when measuring the samples rather than any problems with the equipment.

	Specimen		
	1	2	3
1	2.92	2.89	2.94
2	2.91	2.89	2.94
3	2.92	2.89	2.94
4	2.92	2.89	2.96
5	2.93	2.9	2.94
6	2.92	2.89	2.94
7	2.92	2.89	2.94
8	2.92	2.89	2.94
9	2.91	2.91	2.94
10	2.92	2.89	2.94
11	2.92	2.89	2.94
12	2.92	2.89	2.95

Table 4.3: *Measurements of greatest length (mm) of repeat measurements on 3 randomly selected specimens.*

4.5.2 OBSERVER ERROR

Intra-observer error is assessed using criteria defined by O'Higgins and Jones (1998). Three randomly selected specimens are digitised five times, on 5 consecutive days, then the landmarks from these five repeats were analysed with those of 40 teeth randomly chosen from the same sample population. The combined dataset is then subjected to Procrustes alignment and Principal Component analysis (Fig. 4.2). Fig 4.2 shows the bivariate plot of PC1 and PC2 which account for 31.983 and 14.433 % respectively, accounting for 46.417% of the overall variance within the dataset. The repeated specimens can be seen to form a tight cluster on both PC1 and PC2, with

repeats of each individual specimen being more similar to one another than to any other specimen. This remains true when higher PC's are examined. Figure 4.2 shows an example of intra-observer error in *M. arvalis* as an example. Results show tight clustering of repeated landmark sets for each specimen within all four species of *Microtus* used in this study. This result indicates that the operator errors within the proposed methodology are small with respect to the overall amount of variation observed within a single species sample, and that all species appear to produce similar amounts of inter-observer error, and therefore are unlikely to introduce significant error into the results.

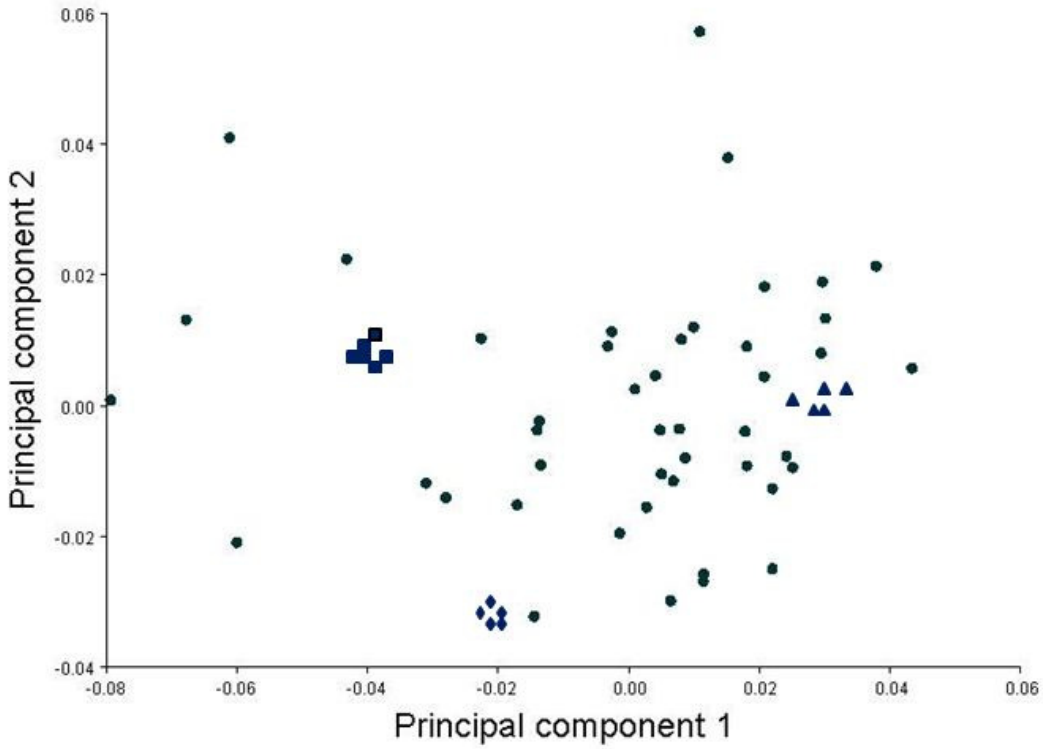

Figure 4.2: *PC1 1 vs. PC 2 of a random selection of modern M. arvalis specimens, with repeated samples of each of the three individual specimens to test error within the sample. Repeated specimens are shown using squares, triangles and diamonds respectively.*

CHAPTER 5
INVESTIGATION INTO THE MORPHOLOGICAL VARIABILITY OF THE M_1 IN MODERN *MICROTUS*

5.1 INTRODUCTION

Morphological features are frequently used to identify species (both extant and extinct) archaeological or palaeontological material as well as reconstructing relationships between them. The use of morphological characteristics to identify species and inter-specific relationships is of particular importance in palaeontology prior to the Late Pleistocene, where the ability to construct genetic phylogenies is limited.

The lower 1st molar is known to be highly variable in *Microtus,* although very little research has been carried out to date on the factors, environmental or genetic, which affect the shape of the lower M_1s. This chapter uses modern *Microtus* material from across Europe to assess factors which may result in morphological differences between populations.

These data are chosen for detailed analysis as the samples are well documented, can be traced back to specific individuals and are all of a similar age (collected from living samples within the last 100 years). Therefore, they are not subject to many of the confounding factors which affect archaeological samples, including taphonomic and temporal change and poor dating resolution. This chapter seeks to explore and understand morphological variability within modern populations, which can then be

applied to the interpretation of archaeological samples. There are four main aims of this chapter, as discussed below.

1) To evaluate the effect of biological factors such as sex and size upon the shape of *Microtus* M_1s.

Sexual dimorphism is common in mammals, and often reflected in skeletal differences between sexes. However, sexual dimorphism is rarely reflected in differences in dentition, other than the presence of increased canine size in males (Hillson, 2005). *Microtus* species do not display a high degree of sexual dimorphism, although males are usually slightly larger (c. 5-15 percent of overall body size) than females (Gromov & Polyakov, 1999). The modern dataset used within this study allows for comparison of morphology in individuals of known sex. The results will then be applied to archaeological material. Therefore, the following hypothesis is erected;

Hypothesis 5.1- *There is no significant difference in the morphology of the lower first molar in male and female Microtus***.**

This hypothesis is tested using comparison of M_1 morphology in known-sex samples.

The genetic and physiological background to dental allometry is discussed in greater detail in chapter 1. Identifying the percentage of variance accounted for by allometry in each of the modern samples, both intra- and inter-specifically, will show if allometry accounts for a similar amount of variation within and between each species. If the amount of allometric variation within the samples is very high, it may be desirable to remove the effect of size upon shape in all subsequent analyses by computing the residuals from the regression of shape on centroid size and therefore removing only

the part of shape variation that is predicted by size variation (e.g. Penin *et al*., 2002; Frost *et al*., 2003; Mitteroecker *et al*., 2004). In order to evaluate the allometric effect on the M_1 in modern *Microtus* species, the following hypothesis is erected;

Hypothesis 5. 2- *There is no significant allometric component to morphological variation in the Microtus* M_1.

The effect of size upon morphology present within the M_1 in each modern *Microtus* species is evaluated by comparing the relationship between size and shape.

2) To test how accurately *Microtus* species can be separated using the shape of the M_1.

The Microtine voles were one of the most rapidly evolving genera in the Quaternary period. This rapid evolution and diversification has meant that *Microtus* remains, particularly teeth (which are often the only well preserved element) have long been of interest to Palaeontologists. In studies of modern material, identification of *Microtus* to species level is possible using mainly soft-tissue features such as fur colour or using elements which are normally not recovered from archaeological deposits, such as cranial morphology. In archaeological or paleontological samples, soft tissue is not preserved and the crania rarely survive intact (Andrews, 1990). Therefore, the element which is most frequently used to differentiate between species in ancient material is their teeth, and this is true of *Microtus* remains. Characteristics of the M_1 traditionally used to identify each *Microtus* species included within this study are discussed in chapter 4.

The high variability in *Microtus* dental morphology has been observed by authors such as Van der Meulen (1974), Gutherie (1965) and Markova and Maul (2001). Currant

(1996) notes that the huge amount of intra-specific variability observed within the highly plastic AC region of the M_1 may lead to inaccurate identification of species when dental morphology is used in isolation. In the case of *M. arvalis* and *M. agrestis*, the dentition cannot be used to separate the two species accurately, as they share a common morphology of the M_1, as defined using traditional identification criteria (Chapter 4). These factors combined with the suggestion that a relatively large proportion of variation in *Microtus* species (between 12- 30%) is not genetically controlled (Polly *et al.*, 2011), suggest that it is important to investigate if the morphology of *Microtus* teeth is, in fact, a definitive species indicator.

. The modern dataset used in this study comprises samples collected from live specimens, and species identification is determined via a range of skeletal and soft-tissue phenotypic characters by experts at the Natural History Museum in London. This allows the accuracy of species identification based upon the morphology of the M_1 to be tested on known-species samples, and then applied to archaeological material. The following hypothesis is erected;

Hypothesis 5.3- *There is no significant difference in the morphology of the lower first molar between different species of Microtus.*

If it is shown to be possible to separate species of *Microtus* accurately using the morphology of the lower 1st molar in H3, the following aim will be investigated:

3) **Evaluation of the effect of missing landmarks on the power species identification in *Microtus.***

Investigating the effect of missing landmarks on the power of species identification using GMM is extremely important. Archaeological material is often subject to

taphonomic influences, which can result in damage to skeletal and dental elements. Although teeth are usually more resistant to taphanomic damage, due to their relatively small size and robusticity compared with other skeletal elements (Hillson, 1999), damage to *Microtus* teeth is common in archaeological assemblages. *Microtus* first molars are particularly prone to damage in the AC region of the tooth due to taphanomic processes (Andrews, 1990). Because the AC region is so variable, it is the main character traditionally used to identify and describe morphological variation between and within *Microtus* species and populations. This leads to an obvious problem when dealing with archaeological material, in which a high percentage of the available specimens are likely to have suffered damage.

The archaeological dataset, for which the species of each sample is definitively known, provides the opportunity to investigate the consequences of missing landmarks upon the ability to distinguish between species. If it is possible to assign specimens to the correct species without the AC region being included within the analyses, there are potential implications for the ability to identify a greater proportion of *Microtus* teeth within an archaeological assemblage than has previously been possible. Therefore, the following hypothesis is erected;

Hypothesis 5. 4- *Excluding landmarks in the AC region of the tooth will prevent separation of Microtus species using the lower first molar.*

If *Microtus* species are shown to be separated with a high degree of accuracy on the basis of M_1 morphology, the ability of Procrustes distances between samples to reconstruct phylogenies will then be evaluated.

4) **To evaluate the possibility of using morphological distances between groups to reconstruct phylogenetic relationships.**

Qualitative descriptions of shape have long been recognised as having systematic value and are often used to describe shape changes in skeletal features. However, the use of quantitative descriptions of shape to form a basis of phylogenetic relationships is more controversial. Geometric morphometric methods, with their ability to analyse the shape of biological structures, provide the potential for phylogenetic relationships to be explored. However, there are several caveats that must be kept in mind in any phylogenetic reconstructions based on morphological data. Firstly, the limitations of geometric morphometrics caused by the requirement for homologous landmarks throughout all specimens mean that researchers are required to select areas of a biological structure which are suitable for landmark placement. Secondly, researchers select areas of the structure or skeletal elements which they *believe* may reflect genetic change, and that assumption may not be correct. Thirdly, any systematic phenotypic variation identified in a biological structure may be a product of several factors, including genetic history and adaptive variation to environmental factors.

Several studies such as those by Collard and Wood (2001) and Rohlf (1998) have led to the argument that morphology is an unreliable indicator of phylogenetic relationships. In these studies, GMM analyses of dental morphology showed no difference between genetically distinct populations or convergent evolution due to environmental constraints. However, many other studies have found a significant correlation between morphology and phylogeny in some closely related species (Cardini, 2003; Polly, 2003). Caumul and Polly (2005) have suggested that molar shape in rodents is a reliable feature to use in phylogenetic reconstructions due to their relatively slow

evolution and the low amount of ecophenotypic morphological variation, leading to a stronger phylogenetic signal being contained within the dentition than other skeletal elements, such as crania or mandibles. They also discovered that, although the relative contribution of mtDNA to molar morphology in Marmots was significantly smaller than that of factors such as diet and body size (5%, 9% and 15% respectively), a strong and reliable phylogenetic signal was recoverable on the basis of M_3molar morphology.

Microtus, as a genus, has been extensively studied in recent years in terms of the relationship between species and the influence of geography on genetic structure of species. The broadest overview of the phylogenetic structure of *Microtus* species to date is that of Jaarola *et al.* (2004). In their study, analyses were carried out on variation in mitochondrial DNA (mtDNA) in 33 species of *Microtus*, including the four species included in this study. Their results suggest there are several distinct and well-supported monophyletic lineages within *Microtus*. *M. arvalis* and *M. agrestis* have a more recent common ancestor with one another than with *M. gregalis* and *M. subterraneus*, which are both more genetically distinct. *M. agrestis* is shown to belong to the Agricola sub-genus, which is similar to the *Microtus* sub-genus containing *M. arvalis*.

M. subterraneus belongs to the *Terricola* sub-genus, confirming the classification of this species into *Terricola* as had previously been suggested on the basis of morphological features (Nadachowski, 1984). However, the study failed to determine the position of *M. gregalis accurately*. This species has been previously been suggested to belong to the subgenus *Terricola*, but the mtDNA results suggest that this subgenus contains several mono-phyletic lineages whose phenotypic morphology is

similar due to adaptive convergence. Palaeontological data suggests an early split of *M. gregalis* from *Allophaiomys* ancestors, with other species evolving at a later date (Rekovets & Nadachowski, 1995). Overall, the phylogeny based upon mtDNA by Jaarola *et al.* (2004) and those based on palaeontological evidence, such as presence/ absence records, first and last appearance of species within the paleontological record and morphological data have a high degree of agreement.

The phylogeography of individual *Microtus* species: *M. agrestis*, *M. arvalis* and *M. subterraneus,* has also been extensively studied (Jaarola & Tegelström, 1995; Jarrola & Searle, 2002; Haynes *et al.*, 2003; Bannikova *et al.*, 2010 and others) and the phylogenetic structure of all three species has been shown to have a strong biogeographic component, with monophyletic lineages occurring within clear geographic boundaries.

This study allows comparison and evaluation of the phylogenies based on M_1 morphology and those gained from genetic data. If phylogenetic reconstructions based upon morphology are shown to be robust, and in line with what is known of molecular phylogenies, the technique will then be applied to extinct data within palaeontological datasets that are not suitable for DNA analysis

The following hypotheses are erected to investigate the phylogenetic signal present within the M_1 of modern *Microtus* species;

Hypothesis 5.5 *Morphological distances between modern species do not reflect the genetic relationships between species*

If H5.5 is rejected, the ability of GMM to reflect intra-species relationships proposed by DNA analysis will be investigated;

Hypothesis 5.6 *Phylogeographic relationships within species of Microtus cannot be reconstructed on the basis of morphological distances between samples.*

5.2 MATERIALS AND METHODS

5.2.1 MATERIAL

The modern dataset comprises 389 individuals; 72 *M. arvalis,* 96 *M. agrestis,* 98 *M. gregalis* and 118 *M. subterraneus*. Table 5.1 shows the provenance of the samples. Matched left and right M_1s are used for comparative purposes, where possible.

Samples are taken from the full geographic range of the species, within the limitations imposed by the scope of the collections. Both left and right teeth are included within all analysis as discussed in section 4.1.

5.2.2 METHODS

The full Modern data set (390 specimens) is used in these analyses, in order to provide a direct comparison to the analyses in H3. Twenty-five landmarks are collected on each tooth, as described in chapter 4, 15 fixed landmarks and 10 semi-sliding landmarks along the curve of the AC region.

In all analyses, landmarks are firstly superimposed using Generalised Procrustes Analysis (GPA) to remove variation due to translation and rotation and to separate shape from size. Further analyses within each hypothesis are as follows:

	M. agrestis			*M. arvalis*			*M. gregalis*			*M. subterraneus*		
Location	♂	♀	**Unknown**	♂	♀	**Unknown**	♂	♀	**Unknown**	♂	♀	**Unknown**
Belgium										4	4	
Turkey							7	8	1	14	13	1
China				4	2	1	20	22	8	2		2
France	6	6	10	8	7	3				10	10	
Germany				7	8	3						
Kazakhstan				12	11							
Norway	8	2	2									
Poland				3	2	1						
Romania										7	3	4
Russia							15	17			3	
Sweden	8	2	8									
Switzerland	18		2							13	12	
UK			10									
Yugoslavia										8	8	
TOTAL	96			72			98			112		

Table 5.1*: Location and composition of datasets included within this chapter. Unknown samples are those for which sex data were not available.*

H 5.1: A Principal Components Analysis (PCA) is performed using the Procrustes-fitted coordinates from the GPA to visualise the major axes of variation within the dataset. A discriminant function with cross-validation is then performed using the Mahalanobis D^2 distances between group means. The use of a discriminant function allows discrimination between groups to be statistically evaluated and therefore to assess if there is any significant sexual dimorphism present in the M_1 morphology of *Microtus* species.

H 5.2: To assess whether there is any significant allometric component to the species datasets, Multivariate regression of shape on centroid size is used. Centroid size is calculated during GPA. Relative warps are used to visualise morphological change related to specimen size.

H 5.3: In order to evaluate if it is possible to identify *Microtus* species on the basis of M_1 morphology, a PCA is performed on the Procrustes-fitted co-ordinates from the GPA analysis in order to see if the major vectors of variation within the sample are aligned with species and a

discriminant function is then performed using the mean group Malahanobis' distances from the GPA to assess the statistical significance of any separation seen during the PCA. Mean shapes are calculated to visualise morphology.

H 5.4: In these analyses, the landmark methodology differs from the standard landmark methodology as described in 4. In order to investigate the effect of missing landmarks in the AC region of the tooth, the semi-sliding landmarks are removed, leaving only the 15 fixed landmarks, as shown in figure 5.1

A PCA is performed on these reduced Procrustes-fitted co-ordinates. A discriminant function is then run to assess the statistical significance of the separation between groups, and this is compared and contrasted with that obtained for the full set of dental landmarks.

H 5.5: A discriminant function analysis is performed to quantify the morphological distance between species. To visualise the relative distances between groups, the unweighted pairgroup method using arithmetical averages (UPGMA) is used to produce phenographic trees showing relationships between species, as explained in chapter 4. The UPGMA trees are calculated using the Procrustes distances between species datasets, which visualises the relative relationships between M_1 morphology for each species. All UPGMA trees are calculated on the basis of the full set of landmarks. The relationships between the species as calculated using M_1 morphology is then compared to that gained from published DNA analyses in order to evaluate if the same relationship is suggested.

H5.6: UPGMA trees are calculated using the method described for H5 for each species separately with the samples grouped by country of origin in order to assess if it is possible to reconstruct phylogenetic relationships within species of *Microtus* using GMM analyses of the lower M_1.

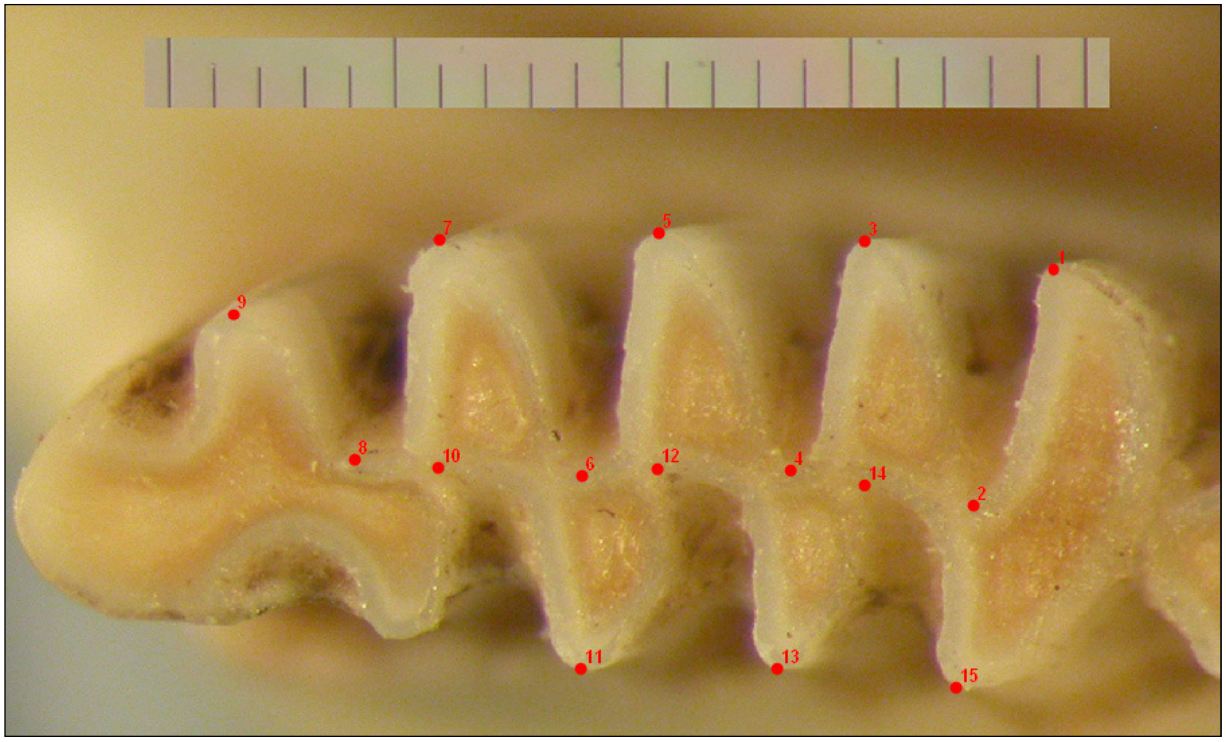

***Figure 5.1**: Location of landmarks in alternative landmark methodology.*

5.3 RESULTS

The following section shows results from all analyses performed on the modern dataset as per the hypotheses outlined above. Results are structured according to the hypotheses being tested.

5.3.1 HYPOTHESIS 5.1: THERE IS NO SIGNIFICANT DIFFERENCE IN THE MORPHOLOGY OF THE FIRST MOLAR IN MALE AND FEMALE *MICROTUS*

Table 5.2 shows the Procrustes distances and associated p-values between male and female individuals of each species as derived from separate analyses of each species.

	Procrustes distance	p-value
M. agrestis	0.02291918	0.7352
M. arvalis	0.01562751	0.5432
M. gregalis	0.02119984	0.6954
M. subterraneus	0.0209706	0.4624

Table 5.2 *Procrustes distances and p-values for each species resulting from a discriminant function analysis*

There is no significant sexual dimorphism in molar shape in any of the species analysed and male and female individuals of the same species of *Microtus* cannot be separated using the morphology of the M_1. On the basis of this evidence, H1 cannot be rejected.

5.3.2 HYPOTHESIS 5.2: THERE IS NO SIGNIFICANT ALLOMETRIC COMPONENT TO MORPHOLOGICAL VARIATION IN THE *MICROTUS* M1.

Multivariate regression of Procrustes co-ordinates onto centroid size is performed for each species in order to summarise any relationship between the size and morphology of the M_1.

Figures 5.2-.5 show shape changes from smallest to largest specimens in each species shown using Cartesian transformation grids as a transformation of the mean shape.

Table 5.3 shows results of the multivariate regression, including percentage of variance explained by allometry and associated p-values. Results suggest *M. agrestis, M. arvalis*

and *M. subterraneus* all display a relatively small allometric component to the morphological variation observed within the sample. For all species, the percentage of variance on PC1 is highly statistically significant (<0.0005). For all species the allometric influence on PC1 is significantly higher than that on PC2; however, the amount of variance explained by allometry on PC 2 is significant for *M. gregalis* and *M. subterraneus*.

The percentage of morphological variance explained by size is much larger in *M. gregalis* than in the other *Microtus* species. For all species, allometry is found to be statistically significant; therefore, H2 is rejected.

	% variance	**p-value**
M. agrestis	6.24	<0.0001
M. arvalis	4.43	0.0001
M. gregalis	20.47	<0.0001
M. subterraneus	7.6	<0.0001

Table 5.3*: Comparison between the percentage of total morphological variance within each dataset explained by allometry, with associated p-values showing the statistical significance of the variance.*

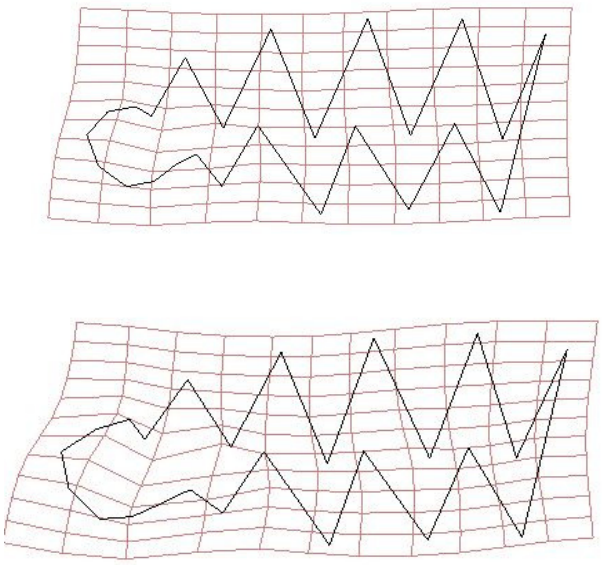

Figure 5.2: *Cartesian transformation grids showing shape change from smallest (top) to largest specimens in the M. agrestis dataset.*

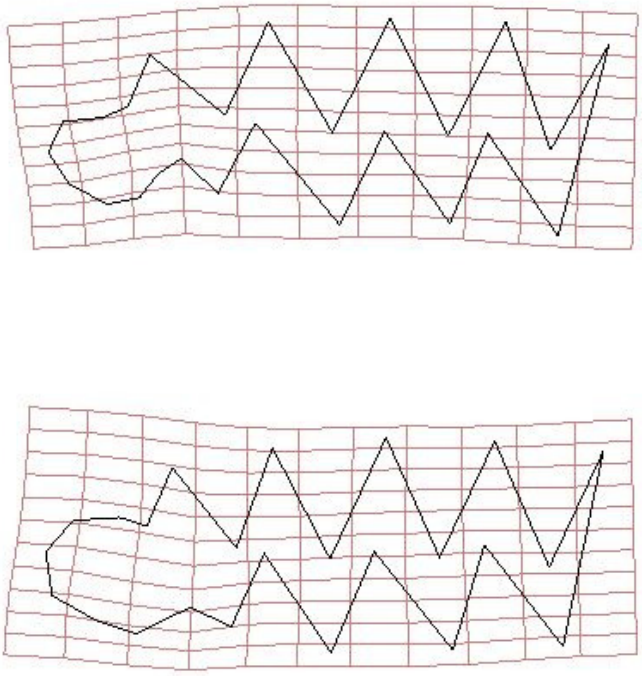

Figure 5.3: *Cartesian transformation grids showing shape change from smallest (top) to largest specimens in the M. arvalis dataset.*

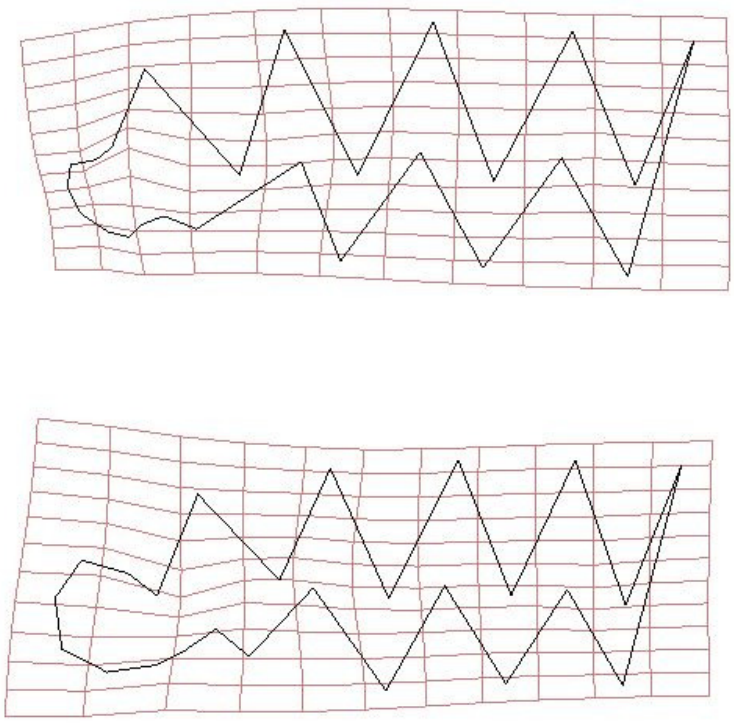

Figure 5.4: *Cartesian transformation grids showing shape change from smallest (top) to largest specimens in the M. gregalis dataset.*

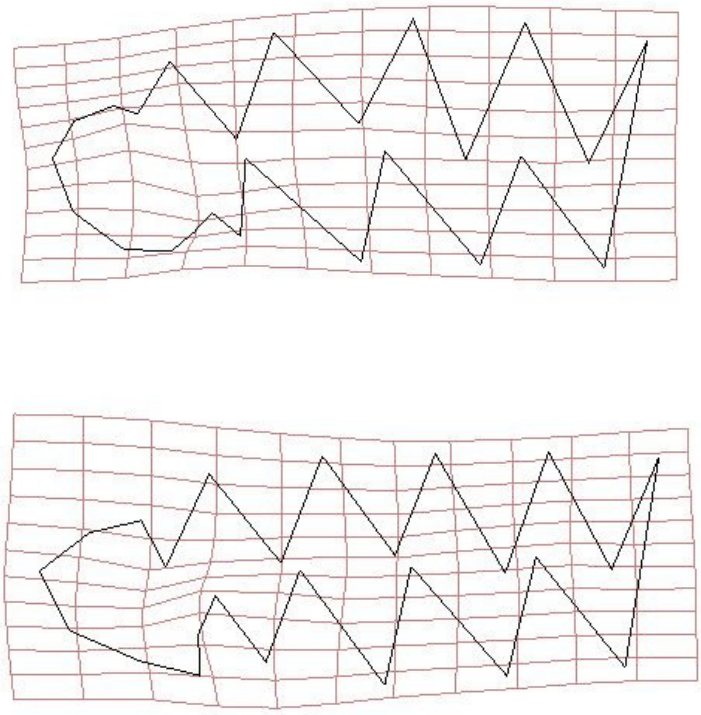

Figure 5.5*: Cartesian transformation grids showing shape change from smallest (top) to largest specimens in the M. subterraneus dataset.*

5.3.3 HYPOTHESIS 5.3: THERE IS NO SIGNIFICANT DIFFERENCE IN THE MORPHOLOGY OF THE FIRST MOLAR BETWEEN DIFFERENT SPECIES OF *MICROTUS.*

Landmarked co-ordinates are Procrustes fitted using GPA and a Procrustes distance matrix is calculated between all individuals within the dataset. A summary of the relationships between individuals is created using Principle Components Analysis.

The first 10 PC's account for 82.156% of the total variance observed within the sample. Eigenvalues and percentage variance explained for each of these Principle components when all *Microtus* species are analysed together are shown in table 5.4

Figure 5.6 shows PC1 vs. PC2, together accounting for 46.432 percent of the total variance, where the species can be observed as broadly separate clusters. The most notable changes across PC1 and PC2, observed through relative warps of the mean shape along the PC (as described in chapter 4), are the relative size of the AC region in comparison with the rest of the tooth and also the orientation of the triangles, with the triangles becoming more or less tilted towards the AC region depending upon species. Mean shapes of each species are shown in figure 5

PC	Eigenvalues	% Variance	Cumulative %
1	0.0016079	35.27	35.27
2	0.0005088	11.16	46.43
3	0.0003891	8.54	54.97
4	0.0002716	5.96	60.93
5	0.0002400	5.26	66.19
6	0.0002132	4.68	70.87
7	0.0001775	3.89	74.76
8	0.0001406	3.09	77.84
9	0.0001073	2.35	80.20
10	0.0000893	1.96	82.16

Table 5.4: *First 10 eigenvalues for a PCA of the modern dataset with percentage of variance within the dataset explained by each PC and cumulative percentage values*

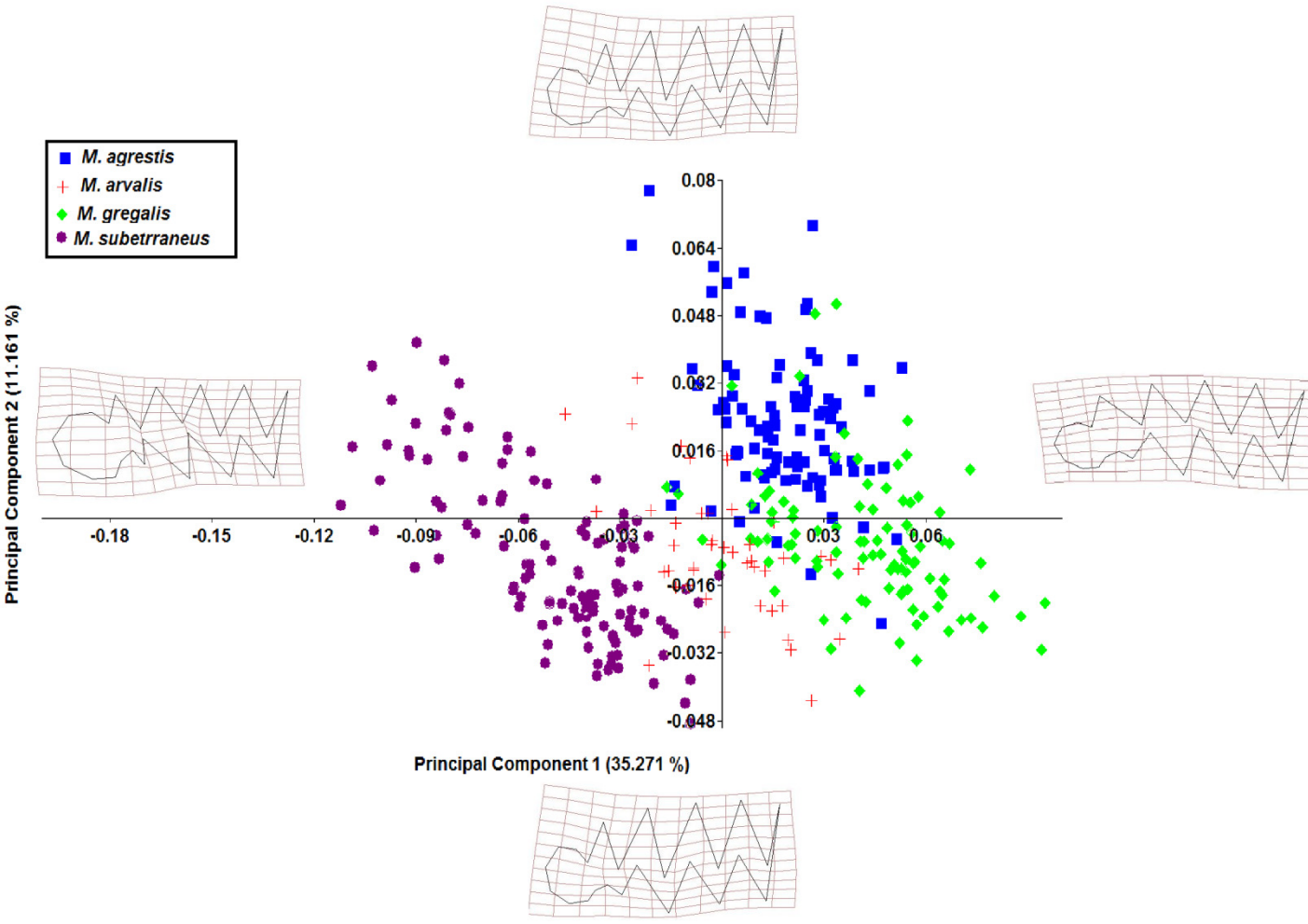

Figure 5.6: *Morphological variation between species of Microtus, as illustrated on PC1 and PC2, with morphological changes at the extreme of each PC illustrated as a deformation of the mean shape of the entire dataset*

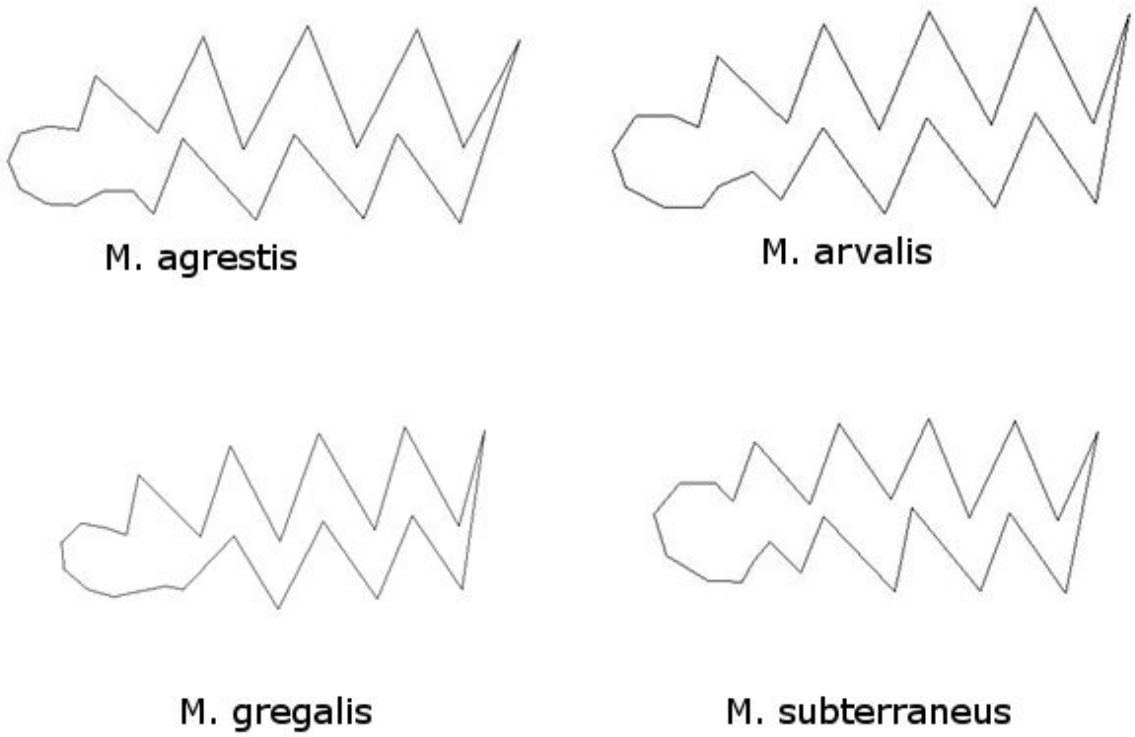

***Figure 5.7**: Average morphology of each species calculated as the mean shape of each Procrustes-fitted sample.*

In order to quantify the significance of the separation between *Microtus* species, a discriminant function with cross-validation is run using the Procrustes co-ordinates calculated in the GPA.

Table 5.5 shows the Procrustes distances between species. *M. subterraneus* is shown to be the species most easily discriminated from the other species within the analysis, with *M. subterraneus* being the most morphologically distinct from *M. gregalis*. Unsurprisingly, given that they cannot be distinguished by eye, it is shown that *M. arvalis* and *M. agrestis* are the least easily discriminated from one another. All Procrustes distances between groups are highly significant (<0.0001), rejecting hypothesis 3 and suggests the morphology of *Microtus* M_1 teeth is species specific to a

highly statistically significant degree. Cross-validation tests between all species are also highly significant at p = <0.001, with each comparison between species leading to > 98 percent of specimens being identified to the correct species. This finding further suggests that *Microtus* teeth of unknown species (I.e.; archaeological samples) could be assigned to the correct species on the basis of morphology.

Having established that it is possible to separate *Microtus* species using the morphology of the M_1, this study now investigates the effect of missing landmarks on the success of discriminating between species based on dental morphology.

	agrestis	***M. arvalis***	***M. gregalis***
M. arvalis	**0.03624663**		
	<.0001		
M. gregalis	**0.05542237**	**0.04996848**	
	<.0001	<.0001	
M. subterraneus	**0.07432034**	**0.05799637**	**0.09752922**
	<.0001	<.0001	<.0001

Table 5.5: *Procrustes distances between Microtus species and associated p-values calculated in a discriminant function analysis (Procrustes distances shown in bold, with associated p-values below).*

	M. agrestis	*M. arvalis*	*M. gregalis*	*M. subterraneus*
M. agrestis	98	2	0	0
M. arvalis	1	99	0	0
M. gregalis	0	0	100	0
M. subterraneus	0	0	0	100

Table 5.6: *Cross-validation results from discriminant function analysis treating all specimens as unknown. Figures are given as a percentage of specimens correctly identified.*

5.3.4 HYPOTHESIS 5.4: EXCLUDING LANDMARKS IN THE AC REGION OF THE TOOTH WILL PREVENT SEPARATION OF *MICROTUS* SPECIES USING THE LOWER FIRST MOLAR.

Figure 5.8 shows the results of a PCA of all specimens, using only the homologous landmarks on the main part of the tooth. Some separation between species can be observed on PC1 and PC2, particularly between *M. subterraneus* and other species. *M. agrestis*, *M. arvalis* and *M. gregalis* have some overlapping specimens, however, distinct groupings for each of the species are still observed, showing clear morphological differences between the species which can be identified using the GMM methodology. The first 10 PCs within this analysis account for 82.032% of the overall variation within the dataset and PC1 accounts for 31.715%. Table 5.7 shows the percentage variance described by each of the principle components

In comparison with samples in which the morphology of the AC region has been included (Fig 4.6) the overall percentage of variance explained by the first 10 PCs is similar.

A discriminant function with cross-validation is then run to assess the significance of the separation between groups. Procrustes distances between groups are shown in table 5.7 with associated p-values.

The Procrustes distances are smaller than those obtained when the AC region of the tooth is included in analyses. However the pattern of relative distances remains the same, with the largest distance between *M. gregalis* and *M. subterraneus* and the lowest between *M. arvalis* and *M. agrestis.*

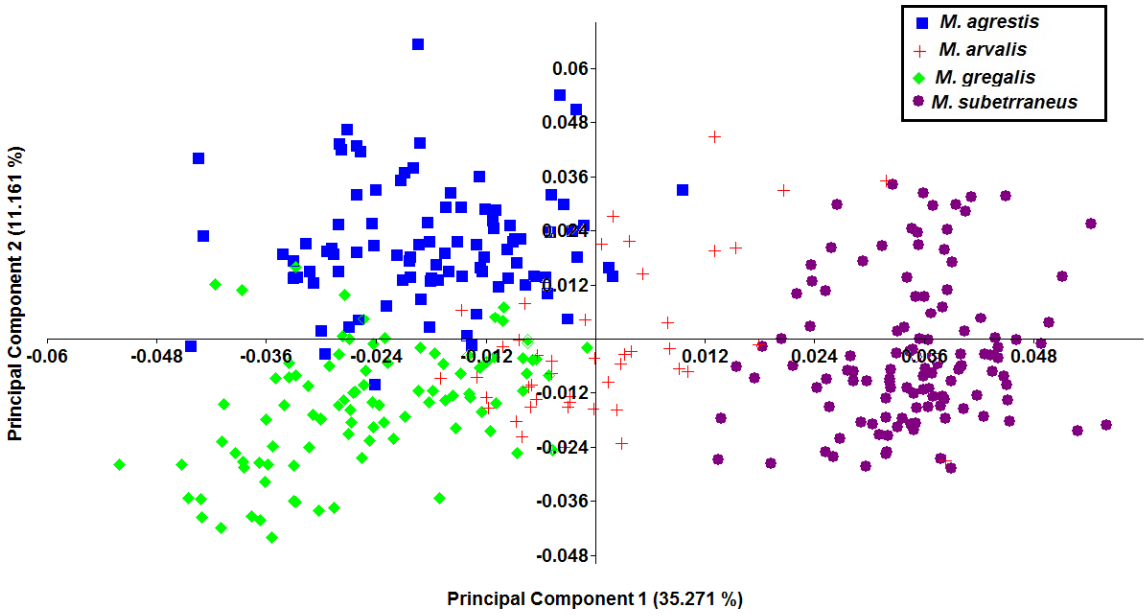

***Figure 5.8**: Morphological variation between species of Microtus (landmark methodology with no semilandmarks) as illustrated on PC1 and PC2.*

	M. agrestis	*M. arvalis*	*M. gregalis*
M. arvalis	**0.04587332**		
	<.0001		
M. gregalis	**0.06601298**	**0.05132157**	
	<.0001	<.0001	
M. subterraneus	**0.09077859**	**0.06669844**	**0.10461187**
	<.0001	<.0001	<.0001

Table 5.7: *Procrustes distances between Microtus species and associated p-values calculated in a discriminant function analysis (Procrustes distances shown in bold).*

	M. agrestis	*M. arvalis*	*M. gregalis*	*M. subterraneus*
M. agrestis	98	2	0	0
M. arvalis	2	98	0	0
M. gregalis	0	0	100	0
M. subterraneus	0	0	0	100

Table 5.8: *Results of a discriminant function analysis including triangular sections of the M_1 only, treating all specimens as unknown. Figures are given as a percentage of specimens correctly identified.*

The p- values for Procrustes' distance between groups= <0.0001, which rejects hypothesis 4 and suggests there is a highly significant species specific morphology of

the *Microtus* triangles 1-5. All species are separated to a highly significant degree (p = <0.001). Cross-validation results show that >98% of all specimens are assigned to the correct species when treated as unknown samples. This result shows only a 1 percent reduction in the percentage of *M. arvalis* correctly assigned when the full landmark methodology was used (table 5.8), and is equal in all other species. Therefore, it can be suggested that exclusion of the AC region of the tooth does not adversely affect the ability to separate species of *Microtus* using the morphology of the M_1 in a discriminant function analysis.

A matrix correlation between the two datasets (15 fixed landmarks and 15 landmarks + 10 semi-landmarks) is performed using the Procrustes distances between individuals within each dataset. The correlation = 0.877179 (p= < 0.0001), which confirms the two differing landmark methodologies produce highly correlated results. Therefore, H4 can be rejected

PC	Eigenvalues	% Variance	Cumulative %
1	0.0016079	35.27	35.27
2	0.0005088	11.16	46.43
3	0.0003891	8.53	54.96
4	0.0002716	5.95	60.91
5	0.0002457	5.26	66.17
6	0.0002132	4.67	70.84
7	0.0001775	3.89	74.73
8	0.0001406	3.08	77.81
9	0.0000893	2.39	80.20
10	0.0000762	1.95	82.15

Table 5.9: *Eigenvalues, proportion of variance and cumulative variance for the first 10 principle components of PCA of modern samples with reduced landmark methodology.*

5.3.5 HYPOTHESIS 5.5- MORPHOLOGICAL DISTANCES BETWEEN MODERN SPECIES DO NOT REFLECT THE GENETIC RELATIONSHIPS BETWEEN SPECIES

As shown in table 5.7, the Procrustes distances between each species of *Microtus* included within this study are statistically significant, indicating that it is possible to separate species with a high degree of accuracy. Procrustes distances (5.7) between the species datasets, calculated during Procrustes' analysis are plotted into a UPGMA tree (figure 5.9). As shown in figure 4.12, the phylogeny created using morphology of the M_1 is broadly comparable to that created using mtDNA (figure 5.10). *M. agrestis* and *M. arvalis* are shown to be the most closely linked species, with *M. gregalis* and *M. subterraneus* show to represent widely separate lineages. Therefore, H5.3.5 cannot be rejected. Further analysis of ability of GMM to reconstruct phylogenetic relationships between species is shown in H6.

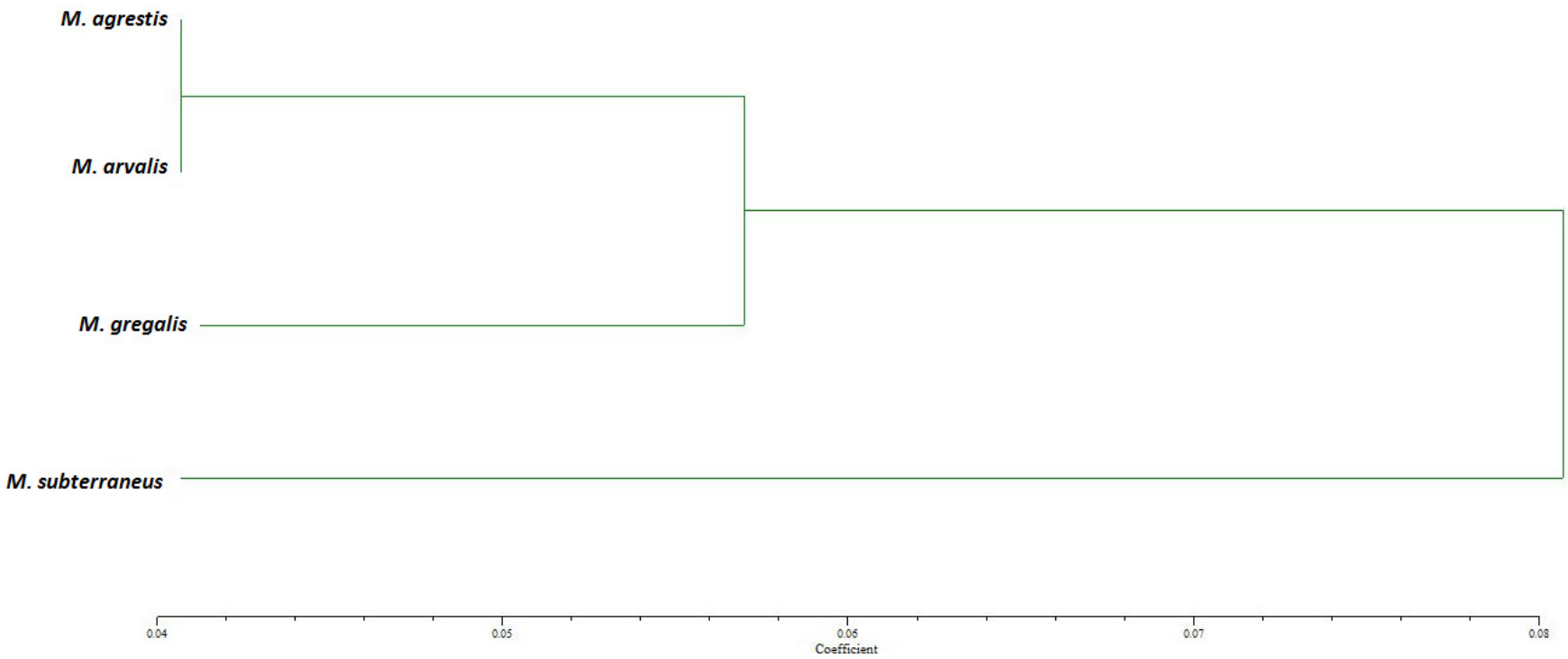

Figure 5.9: UPGMA tree created using Procrustes distances between modern species datasets, showing shape relationships between species.

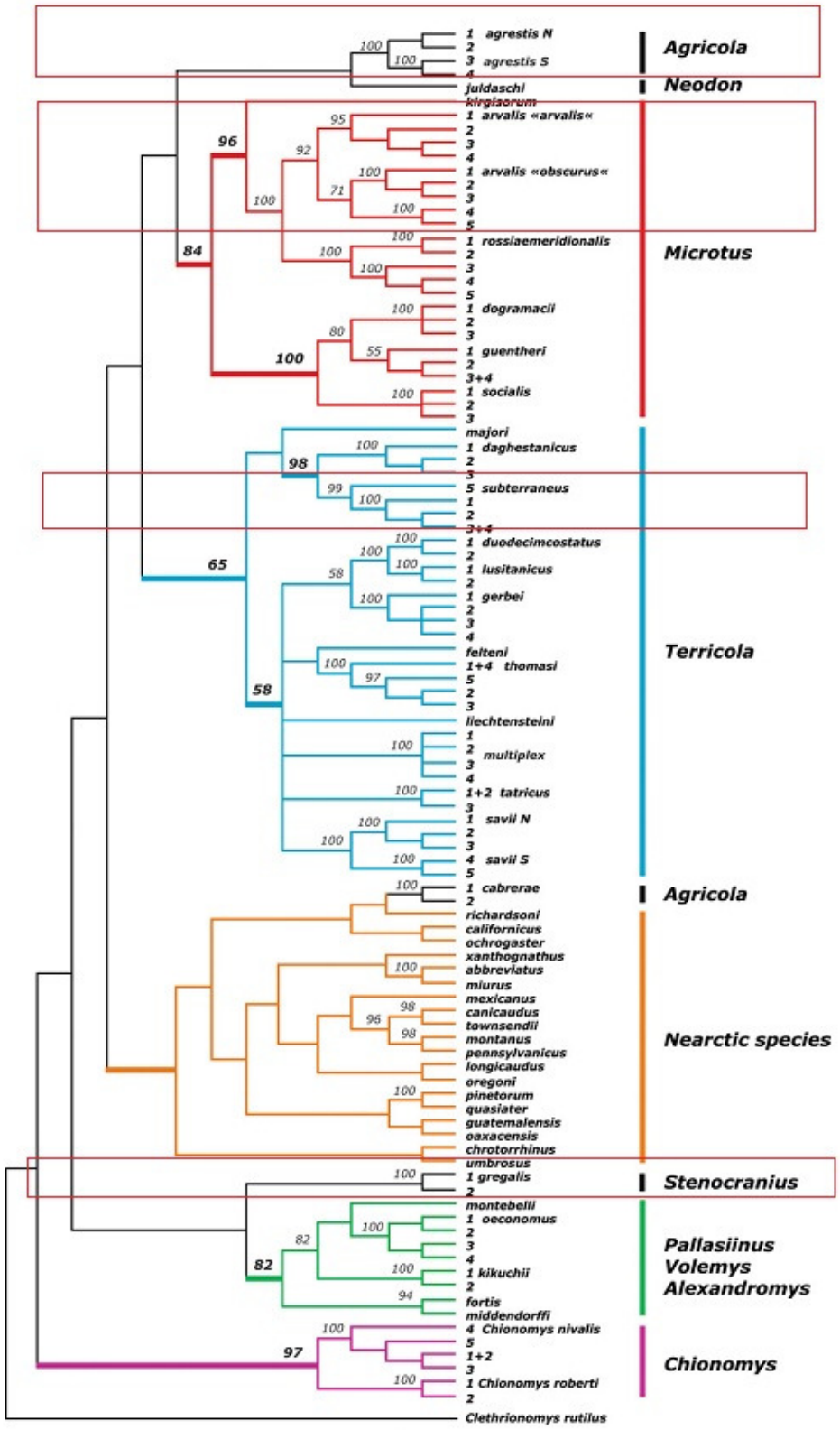

Figure 5.10: *Maximum likelihood tree of inferred cytochrome b phylogenetic relationships between Microtus species. Species included within this study are highlighted in red boxes (Jaarola et al., 2004).*

5.3.6 HYPOTHESIS 5.6- PHYLOGEOGRAPHIC RELATIONSHIPS WITHIN SPECIES OF *MICROTUS* CANNOT BE RECONSTRUCTED ON THE BASIS OF MORPHOLOGICAL DISTANCES BETWEEN SAMPLES.

In this hypothesis, only morphological samples of *M. arvalis* and *M. gregalis* were included due to the lack of published, detailed phylogeographic studies of *M. gregalis* and *M. subterraneus*.

Figure 5.11 shows the morphological distances between samples separated by geographic location in *M. agrestis,* constructed by UPGMA pairing of Procrustes distances between samples. Original Procrustes distances and associated p-values are shown in Table 5.9. For comparison, figure 5.12 shows a phylogeny based upon mtDNA analysis for the same species. All specimens within this sample belong to the Western clade as described by Jarrola and Searle (2002). There are clear similarities between the UPGMA tree based on morphological characteristics and that of the western clade from the published DNA data. Samples from France and Switzerland are closely grouped, as are those from Norway and Sweden, with each pair representing a distinct lineage. Samples from the UK are the most distinct from samples from France and Switzerland and are also shown to be separate (although morphologically more similar) to samples from Norway and Sweden.

Figure 5.13 shows the morphological distances between samples separated by geographic location in *M. arvalis* as constructed by UPGMA pairing of Procrustes distances between samples. For comparison, figure 5.14 shows a phylogeny based upon mtDNA analysis. Original Procrustes distances and associated p-values are shown in Table 5.9. There appears to be a very weak agreement between phylogenies based upon morphological and DNA analyses in this species. The sample from Russia,

corresponding with the '*obscurus*' lineage, the sample from the Netherlands, corresponding with the 'central' clade, the Italian samples and also the UK sample, originating in Orkney, all agree with the DNA data, each being shown in the UPGMA tree as representing a separate lin

The Polish and Hungarian samples are shown to be closely linked and to be separate from the other samples, which corresponds with their position within the Eastern clade in the DNA data. The positions of the French, Spanish and German samples within the UPGMA tree do not correspond with those observed in the mtDNA datasets.

On the basis of the evidence presented above, and the large degree of similarity between UPGMA trees created using morphological distances and published DNA data for *M. arvalis* in particular and to some degree for *M. agrestis*, H6 is rejected.

	France	Norway	Sweden	Switzerland
Norway	0.019869			
Sweden	0.018621	0.014451		
Switzerland	0.017216	0.025598	0.024794	
UK	0.022654	0.019882	0.020036	0.03019657

Table 5.9: *Procrustes distances between samples in M. agrestis by geographical location*

	France	Germany	Hungary	Italy	Netherlands	Poland	Russia	Spain
Germany	0.029762							
Hungary	0.032858	0.028325						
Italy	0.040958	0.032	0.018387					
Netherlands	0.038761	0.03594	0.035291	0.034559				
Poland	0.027557	0.025454	0.026497	0.037019	0.0444415			
Russia	0.048961	0.053799	0.039781	0.047739	0.04584229	0.049619		
Spain	0.024746	0.023556	0.025674	0.029972	0.03938445	0.029277	0.053678	
UK	0.048777	0.039204	0.046852	0.041505	0.04609197	0.053246	0.073506	0.042622

Table 5.10: *Procrustes distances between samples in M. arvalis by geographical location.*

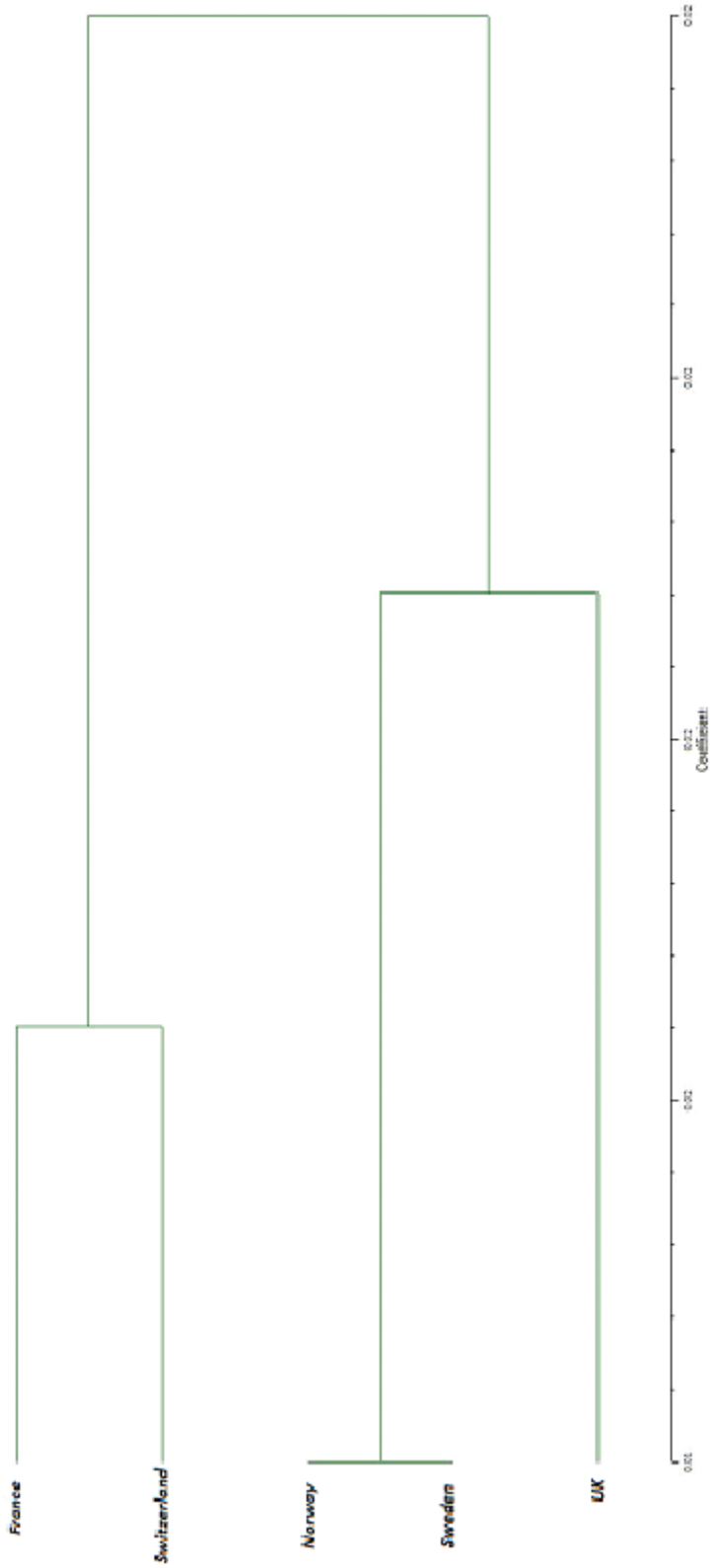

Figure 5.11: UPGMA tree for *M. agrestis* based upon Procrustes distances between group means.

Figure 5.12: *Neighbour-joining tree illustrating cytocrome b analysis of M. agrestis (Jaarola and Searle, 2002, p 2617).*

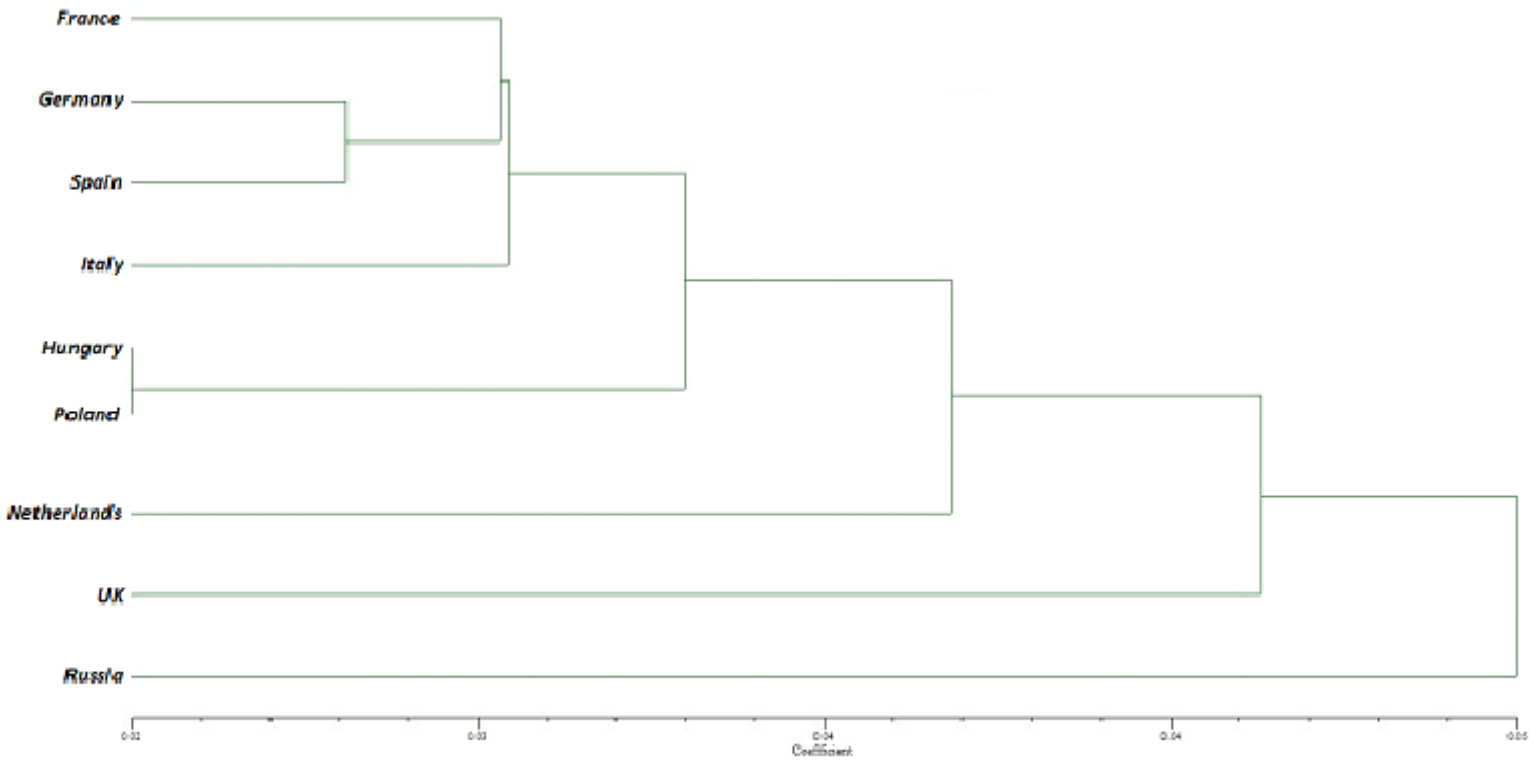

Figure 5.13: UPGMA tree for *M. arvalis* based upon Procrustes distances between group means.

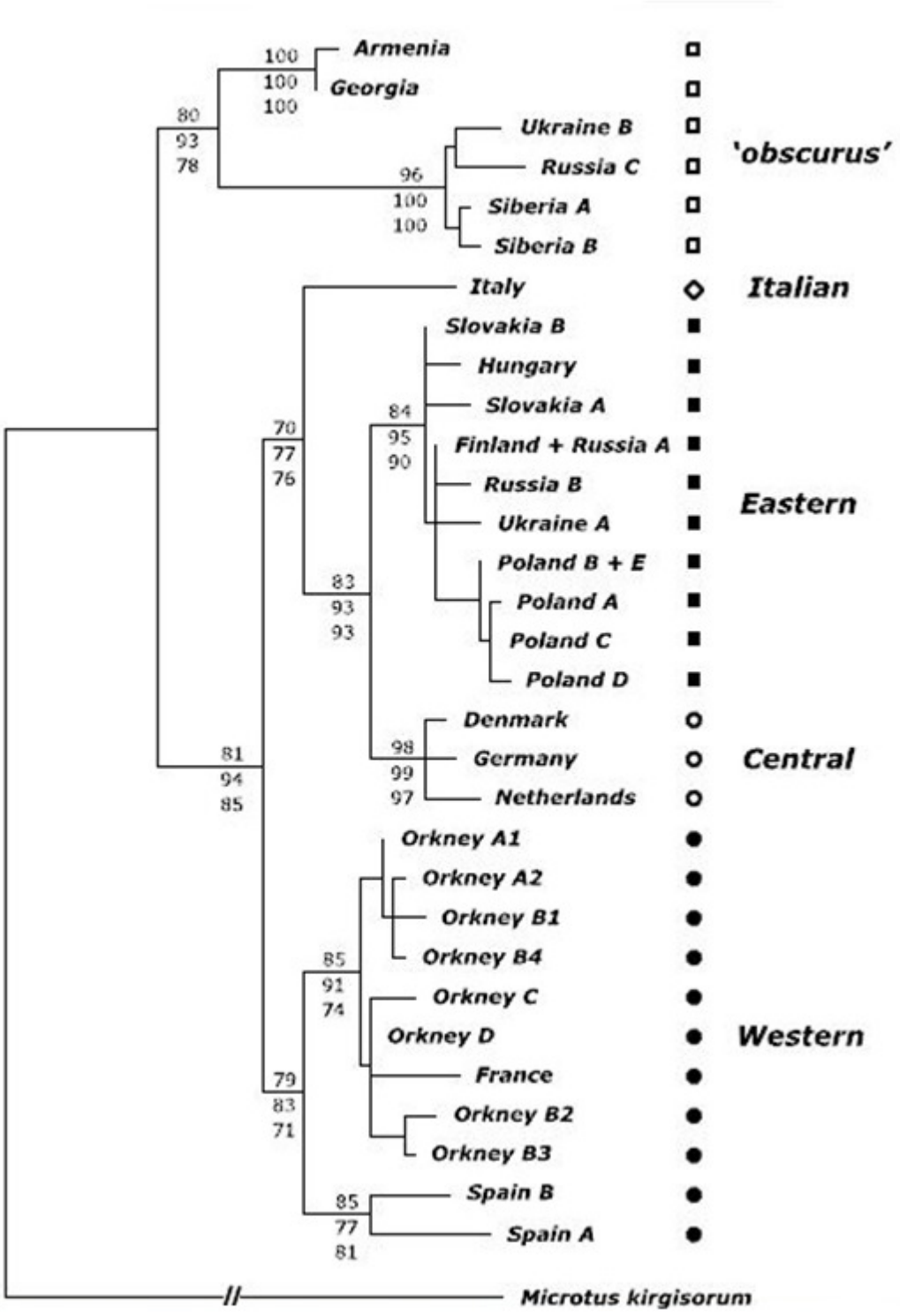

Figure 5.14: Maximum likelihood tree based upon M. arvalis cytochrome b analyses. (Haynes et al., 2003).

5.4 DISCUSSION

The preceding analyses have provided evidence for the effect of size, sex and shape upon the morphology of *Microtus* lower first molars and have examined the degree to which phylogenetic inferences can be made about *Microtus* on the basis of shape data collected using GMM techniques.

Sexual dimorphism in mammals is common, with males usually displaying more robust and larger skeletal elements than those found in females. The effect of this sexual dimorphism is rarely reflected in the dentition of mammals, with the exception of animals that have tusks or large canine teeth, which play a role in sexual selection; however, this is not the case with *Microtus* species. The results of hypothesis H 5.1 suggest that, as is expected given the information above, there is no clear differentiation in the morphology of male and female members of the *Microtus* species included within this study.

Allometry is often used to determine the effect of size upon shape during ontogenetic growth. However, in this study, all samples are from adult individuals and the purpose of investigating the relationship between size and shape of *Microtus* lower first molars is to determine how large an effect shape has on size across populations of each species of *Microtus.* As the results of H 5.2 show, the majority of variation within the dataset is not explained by allometry. The percentage of morphological variation explained by change in tooth size, although not explaining the majority of the variance within the sample is never –the-less highly statistically significant ($p < 0.0005$) for all species. In all species of *Microtus*, M_1 morphology and body size are known to vary in response to both genetic and environmental factors (Schweizer *et al.*, 2007) and therefore, it is not surprising that species datasets which have been sampled from a

wide variety of populations and locations would display a relatively high degree of allometry. The high amount of allometry observed within *M. gregalis* as compared with other species within this study is not presently easily explained. When specimens are identified by country of origin within the regression, there is no clear geographic signal in the dataset, with specimens from all locations displaying a large range of sizes and morphologies. *Microtus* species display a wide variation in body and tooth size; The tooth size range recorded for modern *M. agrestis, M. arvalis, M. gregalis* and *M. subterraneus* are 2.7-3.1, 2,7-3.0, 2.4-2.9 and 2.45-2.8mm respectively (Gromov & Polyakov, 1992). The large proportion of allometry within the dataset may be linked to the fact that *M. gregalis* displays a larger variation in M_1 size than the other species of *Microtus* within this study (Gromov & Polyakov, 2005) and, therefore, can reasonably be assumed to also display a wider variation in tooth size.

In paleontological samples, *Microtus* species are frequently separated on the basis of the morphology of their M_1, with identification criteria focused on the AC region of the tooth in particular (e.g. Van Der Meulen, 1973). Hypothesis H3 is erected to determine the degree to which it was possible to separate known modern *Microtus* species using the morphology of the M_1. Of particular interest was the separation of *M. arvalis* and *M. agrestis*, which have been thought to have extremely similar M_1 morphology and therefore often deemed indistinguishable in paleontological samples (van Kolfschoten, 1991). Results of this study show that all species of *Microtus* studied here can be identified with a high degree of accuracy and assigned to the correct species when their shape is analysed using a discriminant function analysis. For all species, the percentage of specimens correctly assigned to species is highly statistically significant ($p< 0.0001$). Mean shapes of *M. arvalis* and *M. agrestis* (figure 4.11) show that *M.*

agrestis displays a relatively larger AC region and a greater degree of asymmetry in T4 and T5 than *M. arvalis* specimens. This agrees with criteria suggested by Nadachowski (1984) for differentiating the two species; however, GMM methods correctly identify specimens with a hundred percent accuracy. This represents an improvement over the previous method of separation, based upon measurements of the length of the length of the tooth, as these methods only work well in localised populations, but is not of use in samples which differ in size due to temporal, climatic or geographic differences (Nadachowski, 1984). This finding falsifies H 5.3 and suggests that a much greater degree of taxonomic information is present in the shape of *Microtus* M_1 teeth than has previously been suggested when using standard linear measurements or qualitative descriptions to describe shape differences. This finding is highly significant, as there are several potential uses of this technique in palaeoecological reconstructions. Many species of *Microtus* display similar M_1 morphology which is not easily distinguished by eye or through using standard techniques (Gromov & Polyakov, 1992). In some cases, the preferred habitat and climate of similar species may be quite different and the application of these methods could lead towards building more robust palaeoecological and palaeoenvironmental models. There are also clear applications in the field of evolutionary studies, in being able to identify and classify similar material into discrete groups, either in different evolutionary stages of the same species, or in identifying or accurately separating different species.

Hypothesis H5.4 is erected in order to test the effect of missing landmarks upon the ability to differentiate between *Microtus* species. Traditionally, most of the variation between *Microtus* M_1 teeth has been focused on descriptions of the AC region and, therefore, the effect of missing landmarks in this area was evaluated as the AC region

is the region of the tooth which is most frequently damaged in archaeological assemblages (Andrews, 1990). When compared to analysis in H5.3, which included semi-landmarks on the AC region of the tooth, the Procrustes' distances between species are slightly smaller in the analysis where the AC region was not included; however, the p-values gained from the discriminant function analysis ($p=<0.0001$) for all specimens suggest it is possible to exclude landmarks in the AC region of the tooth and separate species with a high degree of accuracy. H5.4 is therefore refuted.

This finding is important, as it suggests there is a far larger degree of morphological variability in the non-AC regions of the M_1 than had previously been recognised, and that this variability is species specific. The results of these analyses have potential applications in palaeontological assemblages where it may be important to determine relative species frequencies, but in which a large proportion of teeth have suffered damage.

The accuracy of constructing a phylogeny based upon morphological characteristics of the M_1 is assessed in hypotheses 5 and 6. The results show that a limited phylogenetic signal is recoverable from molar morphology. Results of H5.5 show that molar shape has promise in the construction of inter-specific relationships between species of *Microtus. M. agrestis* and *M. arvalis* are shown to have the closest relationship in both the phylogeny based on morphology and in that based on mtDNA. In phylogenies, *M. subterraneus* and *M. gregalis* are seen as separate lineages to the *M. arvalis*/ *agrestis* lineage. However, the phylogenies differ in their placement of *M. gregalis*. In the molecular phylogeny, *M. gregalis* is widely separated from all the other species whereas in the morphological phylogeny, *M. gregalis* is shown to be more similar in shape to *M. arvalis* and *M. agrestis* with *M. subterraneus* being the most divergent

species. As the AC region in *M. arvalis*, *M. gregalis* and *M. subterraneus* are very similar morphologically, it can be suggested that the feature which is causing *M. subterraneus* to be separated most widely from the other species is the presence of the 'pitymoid' feature- i.e.; T4 and T5 being broadly confluent. As this feature has been suggested to be a morphological developmental stage through which all *Microtus* species evolve (Markova & Maul, 2007), this feature is not necessarily genetically informative in itself.

The possibility of using morphology to reconstruct palaeogeographic relationships between samples is thus great, as shown in tests of hypothesis 6.

5.5 CONCLUSIONS

To summarise the data and discussion above, the major findings of this chapter are summarised as thus;

- Sex has no significant effect on the morphology of the M_1.
- Allometry does affect the shape of *Microtus* M_1s, in *M. arvalis*, *M. agrestis*, *M. gregalis* and *M. subterraneus*. Between *Microtus* species, the effect of size on dental morphology appears to vary. However the majority of variation within the sample is be explained by factors other than allometric influence.
- Separation of species of *Microtus* included within this study is possible with a high degree of accuracy via analysis of the morphological differences in the shape of the M_1. Specimens are identified correctly during cross-validation >98 percent of the time in all cases.

- *M. arvalis* and *M. agrestis* can be separated with a high degree of accuracy, which is not possible using standard techniques, and therefore has important implications in fossil material. Specimens are correctly identified with approximately 98 percent accuracy.
- When landmarks in the AC region of the M_1 are missing, it is possible to use landmarks only on T1-T5 to distinguish between species accurately, suggesting a larger amount of taxonomic information and morphological variation is present within T1-T5 than was previously suggested.
- Relationships between and within species of *Microtus* constructed using M_1 morphology have a high degree of accuracy when compared with phylogenetic relationships as constructed using DNA analyses

CHAPTER 6
CASE STUDY 1- WALOU CAVE

6.1- INTRODUCTION.

Chapter 4 identifies that, in modern material, species can be readily identified using several different landmark configurations. Allometry, sexual dimorphism and intraspecific variation in the shape of *Microtus* lower first molars were investigated, and the impact of missing landmarks upon the results is shown to be small.

The present chapter will build on these analyses and attempt to address temporal factors of shape variation, which cannot be investigated in a modern dataset. It will do so by analysing data from a single archaeological site, with a long stratigraphic sequence: Walou Cave.

The fragmentary nature of palaeontological remains, and the difficulties associated with understanding the stratigraphic relationships within a site mean that any attempt to understand how geometric morphometric techniques might be applied to *Microtus* teeth in relation to climatic and stratigraphic questions, must first be tested on material where the stratigraphic sequence and climatic changes throughout the sequence are well understood. This chapter will apply the geometric morphometric protocol outlined in chapter 3 to such a dataset and explore patterns of variation related both to temporal position and climatic change.

Walou Cave is one of the best studied sites in the late Pleistocene of Belgium. The cave provides an unparalleled sedimentary sequence from MIS 6 through to the Holocene. The cave´s importance lies in the presence of archaeological remains and artefacts in

many of the stratigraphic levels as well as the presence of significant quantities of both large and sm

Mammalian remains throughout the sequence. Neanderthal remains have been found in association with Mousterian tools at one stratigraphic level within Walou, further raising the importance of the cave (Pirson et al., 2006). Detailed description of the sediments, mammalian remains and palaeoenvironmental reconstruction at Walou Cave can be seen in Chapter 6.

Due to the long sequence of sediments at Walou Cave, covering c. 120,000 yrs, the site represents an ideal case study for the application of geometric morphometrics in reconstruction of climatic data and as a tool for the study of stratigraphic and temporal relationships. The presence of two tephra horizons within the stratigraphic sequence, combined with C14 and thermoluminescence dates correlated with Loess stratigraphy throughout Belgium, means that the age of the stratigraphic sequence at the site is extremely well understood and well constrained. Palynological and mammalian remains have also been studied intensively at the site, providing information on climatic change both at Milankovich and sub-Milankovitch scales (Parfitt and Stewart, 2009, Pirson et al., 2006). The present chapter will thus assess the degree to which external environmental and temporal factors can be seen to affect the shape of *Microtus* M_1s from a single geographical location through time.

The present chapter assesses the degree to which temporal and environmental factors determine the patterns of morphological diversity in *Microtus at* Walou Cave by examining the following main aims:

1) **Evaluation of the effect of size on the shape of *Microtus* M_1 teeth.**

As discussed in chapter 1, allometry is morphological variation that is associated with, or caused by variation in size. It is important to assess the degree of allometry present within the M_1 of the *Microtus* species included within this study, as if a large allometric component is found within the data, it may be desirable to remove is before subsequent analyses (e.g. Penin et al., 2002; Frost et al., 2003; Mitteroecker et al., 2004).

The Modern dataset (analysed in chapters 4 of this study) demonstrates statistically significant allometric components within the species datasets, in most cases accounting for c. 5% of the variance observed within PC1. This dataset includes samples from a wide geographic range. The samples from Walou Cave are significantly more constrained geographically, as they contain samples from a single site. Therefore, the relative proportions of allometry displayed in Walou Cave samples may be of interest in comparison with the Modern datasets.

Therefore, the following hypothesis is erected;

Hypothesis 6.1: - *There is no significant allometric component to intraspecific diversity in Microtus lower M_1 morphology at Walou Cave.*

2) **Evaluation of the degree of morphological change present through the stratigraphic sequence at Walou Cave.**

As discussed in detail within chapter 1, *Microtus* species are known to evolve extremely rapidly, and this evolution is reflected in their dental morphology (Chaline et al., 1999). This provides the potential for dental morphology in *Microtus* species to be used as a relative dating method of sediments. However, this is an area that has not been studied in any detail in *Microtus* species, unlike in other closely-related Microtine rodents such as *Arvicola*/ *Mimomys* (Von Kolfschoten & Van Koeningswald, 1996; Von Kolfschoten, 1990).

Evidence of morphological change, in terms of shape or size, throughout the sequence may represent rapid evolution within a single population, population dispersal or replacement. As the time period represented by the *Microtus* remains from the Walou Cave sediments is thought to be relatively short, representing part of a single interglacial cycle, it may be expected that there will be little or no morphological evolution through the sequence. Rapid diversification and evolution of distinct M_1 morphologies have been identified within separate populations of *Microtus* in the Orkney Isles. This rapid differentiation of populations occurred from the initial introduction of *Microtus* to the islands in the Neolithic to the present day, suggesting the possibility of rapid morphological change in *Microtus* species over short time-frames (Corbet, 1986). However, a generalised model of the rate of dental evolution in *Microtus* species has not, to date, been studied. The following hypotheses are erected to investigate morphological change throughout the stratigraphic sequence at Walou Cave;

Hypothesis 6.2*: There is no significant intra-specific variation in Microtus lower* M_1 *tooth size throughout the stratigraphic sequence at Walou Cave.*

Hypothesis 6.3- *There is no significant intra-specific variation in Microtus lower M_1 tooth shape throughout the stratigraphic sequence at Walou Cave.*

If a significant amount of variance in size or shape between stratigraphic levels is found, the following hypothesis will be erected to evaluate if size and shape are linked throughout the dataset;

Hypothesis 6.4: *There is no significant difference in intraspecific variation in both size and shape of Microtus lower M_1 throughout the stratigraphic sequence at Walou cave.*

3) Evaluation of the effect of external environmental factors, such as prevailing climate on the morphology of the *Microtus* M_1.

An alternative explanation for morphological change in shape or size of *Microtus* teeth through the stratigraphic sequence at Walou Cave is the influence of climatic factors upon epigenetic variation. Several studies have shown that *Microtus* teeth display a relatively low degree of epigenetic variation (Uhlikova, 2004). However, distinct morphological changes in the morphology of *Microtus* dentition attributed to climatic change have been demonstrated in more than one study (Montuire et al., 2004; Mc Guire, 2009). *Microtus* species have also been shown to increase in size in warmer conditions and decrease in cooler ones, the opposite of what might be predicted by Bergmans' Rule (Bergman, 1847). Therefore, it is possible that the size of *Microtus* teeth may also change in line with general body-size change in response to the prevailing climatic conditions.

The climatic conditions for each stratigraphic level at Walou Cave are well understood, and the sequence records a decline from wooded, vegetation- rich temperate conditions into cool, open and arid conditions (Roberts & Parfitt, 1999) over a relatively short space of time. Therefore, it may be possible to identify specific morphological changes or changes in size in *Microtus* species that are associated with climatic conditions. To investigate the effect of climate upon morphology within the Walou Cave dataset, the following hypotheses are erected

Hypothesis 6.5: *There is no significant difference in the intraspecific variation of size in Microtus lower M_1 teeth at Walou Cave caused by climate.*

Hypothesis 6.6: *There is no significant difference in the intraspecific variation of shape in Microtus lower M_1 teeth at Walou Cave caused by climate.*

6.2 MATERIAL AND METHODS

An outline of the number and stratigraphic location of specimens, plus the methods of analysis used within this chapter are provided below;

6.2.1 MATERIAL

The Walou cave sample is comprised of 183 specimens of *M. arvalis*, *M. agrestis* and *M. gregalis* from eight stratigraphic levels (Table 6.1). Material was collected in excavations between 1997 and 2002 and specimens were extracted from sediment samples that were specifically selected for microfaunal analysis. Samples were sieved using a 1mm mesh and the resulting residues were sorted by eye for small vertebrate remains. All *Microtus* teeth should have been retrieved from the samples as their teeth are larger than 1mm in size (Parfitt and Stewart, unpublished). Many of the specimens

within the samples recovered from Walou Cave are damaged and therefore cannot be included within these analyses, resulting in reduced sample sizes.

	A6	B2	B5	C1-6	C1-8	C2	C4	D
M. arvalis/ agrestis	11	13	10	35	36	9	12	16
M. gregalis	2	8	3	0	0	5	0	0

Table 6.1: *Number of specimens recorded at Walou Cave according to species and stratigraphic location.*

6.2.2 METHODS

The size of the Walou cave sample is relatively small when separated by stratigraphic level and the only species present in large enough numbers to produce statistically valid analyses across several stratigraphic levels are *M. arvalis/ agrestis.* This presents a problem, as the M_1 morphology of *M. arvalis* and *M. agrestis* cannot be discriminated by eye and previous research has not looked for the presence of M_2 teeth, which would allow species identification.

As shown in chapter 4, it is possible to separate modern specimens of *M. arvalis* and *M. agrestis* with a high degree of accuracy (p=< 0.0001) using GMM techniques. As the separation of the two species using modern material is highly statistically significant, a discriminant function is generated between the known groups of modern material and this discriminant function and then used to assign the unknown archaeological material to either *M. arvalis* or *M. agrestis*

To test the stability of this approach, the unknown Walou samples are assigned to species on the basis of discriminant functions generated from two separate modern datasets. The first dataset consists only of modern *M. arvalis* and *M. agrestis* samples as the morphology of these species, although difficult to separate from one another is distinct from *M. gregalis* and *M. subterraneus* and therefore there is a high degree of likelihood that all the unknown specimens do in fact belong to *M. arvalis/agrestis* rather than being mistakenly identified members of another species. Modern sample sizes of *M. arvalis* and *M. agrestis* contain 45 and 94 specimens respectively. Secondly, the unknown *arvalis/ agrestis* samples are added to a discriminant function consisting of all 4 modern species: *M. arvalis, M. agrestis, M .gregalis* and *M. subterraneus* (45, 94, 100 and 118 specimens respectively). All modern specimens are taken from a range of geographic locations (see table 5.1 for detailed sample locations).

The unknown samples are given an equal prior probability of belonging to each of the groups (25% or 50 % for full modern or *M. arvalis/ agrestis* samples). Each test is carried out twice, once including the semi-landmarks around the AC region, and once using only the homologous landmarks to evaluate the effect of removing the AC region of the tooth.

As can be seen in Appendix 1, each methodology produced extremely similar results, which suggests that the discriminant function is extremely robust when assigning unknown samples to either *M. arvalis or M. agrestis*.

Species composition after assignment of *M. arvalis*/ agrestis samples can be seen in table 6.2.

	A6	B2	B5	C1-6	C1-8	C2	C4	D
M. arvalis	10	9	8	30	27	7	12	14
M. agrestis	1	4	2	5	9	2		2
M. gregalis	2		3			5		

Table 6.2: *Sample sizes for each species at Walou Cave after M. arvalis and M. agrestis have been separated using discriminant function analysis.*

All specimens are recorded using photographs and 15 homologous landmarks placed on each specimen, with a further 10 semi-landmarks placed around the AC region of the tooth to fully capture the shape variation within the samples (Figure 3.2). All analyses of shape are conducted using the full set of landmarks.

In all analyses, specimens are firstly superimposed using Generalised Procrustes Analysis (GPA) to remove the effects of size, translation and orientation upon the dataset prior to further analysis. During GPA, the centroid size of each specimen is calculated and is then retained for use in further analyses, as discussed below. Further methods of analysis within this chapter are outlined below;

H 6.1: In order to assess the allometric component to the species datasets, a multivariate regression of shape co-ordinates on centroid size is performed, using centroid sizes and shape coordinates. Centroid sizes are calculated during Procrustes' fitting and are used as a measure of size, as they are a biologically meaningful expression of the overall scale of the landmark configuration. Shape change is visualised as Cartesian Transformation Grids calculated using thin plate splines.

Due to the small specimen numbers present within the Walou cave dataset, *M. agrestis* and *M. gregalis* are not judged to be suitable for further analyses, so all other hypotheses are performed only upon the *M. arvalis* dataset.

H 6.2 & H 6.5: To calculate if there is a statistically significant difference in a Students' t-test is performed upon the centroid sizes of each sample, as calculated during the Procrustes fit of the combined samples.

H 6.3 & H 6.6: Principal Components Analysis (PCA) is performed using the Procrustes-fitted coordinates from the GPA, to visualise the major axes of variation in the dataset. To investigate the variation within the datasets further, a discriminant function is performed using the Mahalanobis D2 distances between group means. To assess the power of the discriminant function, a discriminant function with leave-one- out cross-validation is carried out. To visualise the relative distances between groups, the unweighted pairgroup method using arithmetical averages (UPGMA) is used to produce phenographic trees showing relationships between species, explained in chapter 3. The UPGMA trees are calculated using the Procrustes distances between species datasets. All UPGMA trees are calculated using the landmark methodology on the basis of the full set of landmarks, as shown in chapter 3. A range of variance values is then calculated via bootstrapping the original data 1000 times. The bootstrap value are then plotted to provide curves illustrating the distribution of variance in shape-space for each sample.

H 6.4 & H 6.7: In samples where there appears to be a difference in both shape and size, samples are analysed in Procrustes' Form-space. Log centroid size is included within a Principle Component Analysis of Procrustes-fitted coordinates. In order to

investigate the variation within the datasets further, a discriminant function is performed using the Mahalanobis D2 distances between group means. To assess the power of the discriminant function, a discriminant function with leave-one- out cross-validation is performed.

6.3 RESULTS

Results of all analyses on the Walou cava dataset are summarised below, according to the hypothesis being tested.

6.3.1 HYPOTHESIS 6.1: - THERE IS NO SIGNIFICANT ALLOMETRIC COMPONENT TO INTRASPECIFIC DIVERSITY IN *MICROTUS* LOWER M_1 MORPHOLOGY AT WALOU CAVE.

Multivariate regression of Procrustes co-ordinates onto centroid size is performed for each species in order to summarise any relationship between the size and morphology of the M_1. Full centroid sizes for all individuals are provided in appendix C.

Table 6.3 shows that, in the *M. agrestis* and *M. gregalis* datasets, a high proportion of the overall shape variance within the dataset is explained by the size of the tooth (approximately nine percent). However, both datasets are very small, comprising 17 and 24 individuals respectively, which may produce bias within the results (Wardlaw, 2000). Both datasets are, however considered to have a statistically insignificant allometric component (*M. agrestis* p= 0.1360 and *M. gregalis* p= 0.0899). The *M. arvalis* dataset (116 individuals) is calculated to have a greatly reduced allometric component in comparison with the other Walou cave species datasets, with 2.7998 percent of the variance in shape being explained by change in size. This result is found to be statistically significant (p= 0.0004). Figure 6.1 illustrates the change in shape between the largest and smallest *M. arvalis* specimens. Smaller specimens of *M.*

arvalis at Walou Cave are shown to have an AC region that is tilted towards the posterior of the tooth, compared with the larger specimens where the AC is tilted towards anterior. In smaller specimens, the buccal re-entrant angle is also more pronounced in smaller specimens than in larger. Although the result for *M. arvalis* is found to be significant, the percentage of variation within the dataset explained by allometry remains low, and therefore does not need to be removed in further analyses. On the basis of the evidence presented above, H 6.1 cannot be rejected.

	Total % predicted	**p-value**
M. agrestis	9.0575	0.1360
M. arvalis	2.7998	0.0004
M. gregalis	9.5271	0.0899

Table 6.3: Comparison between the percentage of total morphological variance within each dataset explained by allometry, calculated using multivariate regression of Procrustes co-ordinates onto centroid size, with associated p-values showing the statistical significance of the variance (statistically significant results are highlighted in yellow.)

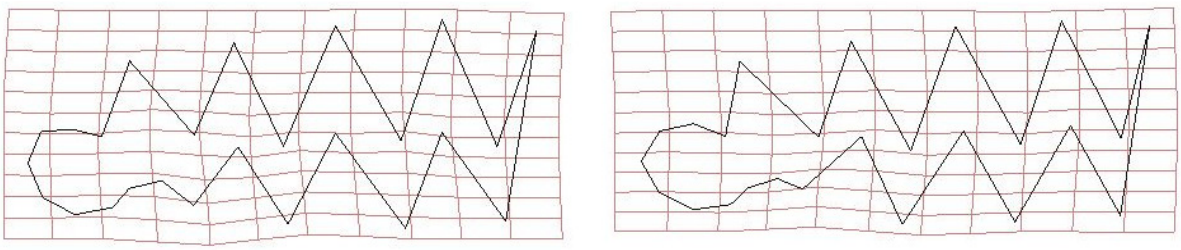

Figure 6.1: *Comparison of shape in smallest (left) and largest (right) specimens of M. arvalis at Walou Cave, as calculated using relative warps of thin plate splines.*

6.3.2 HYPOTHESIS 6.2: THERE IS NO SIGNIFICANT INTRA-SPECIFIC VARIATION IN *MICROTUS* LOWER M_1 TOOTH SIZE THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT WALOU CAVE.

In order to assess differences in size throughout the stratigraphic levels at Walou cave, a Students' t-test Is performed on the centroid sizes of specimens from each stratigraphic level (as calculated during GPA) to determine if there is a significant difference in the mean size of each group. Table 6.4 shows the resultant t-values and the associated p-values (Centroid sizes for all individuals can be seen in appendix C). As can be seen from the results, there is a statistically significant difference in size between most stratigraphic levels. There does not appear to be any linear trend in size throughout the stratigraphic sequence, as stratigraphic levels which are furthest apart temporally do not necessarily have the most significant difference in size. Where non-significant differences in size are reported, the results do not appear to be an artefact of sample size (for sample sizes by stratigraphic level, please refer to table 6.2). Mean centroid sizes for each stratigraphic level can be seen in table 6.5 and show that mean size fluctuates throughout the sequence rather than increasing over time as suggested by Allroy (1998). On the basis of this evidence, hypothesis H 6.2 cannot be rejected.

	A6	B2	B5	C1-6	C1-8	C2	C4
B2	**-4.63676**						
	<0.0001						
B5	**1.184068**	**5.327129**					
	0.246793	*<0.001*					
C1-6	**3.282855**	**8.002342**	**1.98615**				
	0.001753	*<0.0001*	*0.050919*				
			-	-			
C1-8	**-1.25274**	**3.994968**	**2.322298**	**5.072525**			

	0.021723	*0.000329*	*0.025261*	*<0.0001*			
			-	**-**			
C2	**-2.11141**	**2.094733**	**2.947919**	**5.026718**	**-1.17722**		
	0.044505	*0.04061*	*0.00342*	*<0.0001*	*0.024683*		
				-			
C4	**1.145431**	**4.560877**	**0.207574**	**1.447618**	**2.155668**	**5.565779**	
	0.261727	*0.00019*	*0.83712*	*0.153614*	*0.037507*	*0.01763*	
			-	**-**			
D	**-0.43883**	**3.928968**	**1.519004**	**3.477503**	**0.723432**	**1.600697**	**-1.39626**
	0.664039	*0.00077*	*0.139973*	*0.001008*	*0.473731*	*0.123091*	*0.174912*

***Table 6.4**: Results of a Students' t-test of M. arvalis centroid size throughout stratigraphic levels at Walou Cave. T-values are shown in bold and associated p-values in italics. Statistically significant results are highlighted in yellow.*

Level	Mean Size
A6	2264.3814
B2	2616.6501
B5	2218.314
C1-6	2149.7516
C1-8	2324.2665
C2	2421.1486
C4	2207.9565
D	2287.6019

Table 6.5: Mean centroid size for samples from each stratigraphic level at Walou Cave.

6.3.3 HYPOTHESIS 6.3- THERE IS NO SIGNIFICANT INTRA-SPECIFIC VARIATION IN *MICROTUS* LOWER M_1 TOOTH SHAPE THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT WALOU CAVE.

In order to assess the degree of differentiation in the shape of the M_1 within species through the stratigraphic sequence, PCA is performed on the Procrustes fitted data of *M. arvalis.*

Figure 6.2 shows the bivariate plot of PC 1 and PC 2, cumulatively accounting for 29.527 percent of total variance (Complete eigenvalues can be seen in table 6.6). It is clear from these figures that there is no separation of the samples on PC1 and PC2. This remains true of further Principal components, with no separation between stratigraphic groups observed on any combination of Principal Components.

In order to explore further any differences in morphology between *M. arvalis* from different stratigraphic levels, a discriminant function analysis is performed. Table 6.8 shows the results of the discriminant function analysis. In all stratigraphic levels, the variation in shape between stratigraphic levels is found to be highly insignificant ($p>0.05$). Samples which are more temporally distant do not show a greater Procrustes distance between samples than those which have smaller temporal separation. Table 6.8 shows the results of cross-validation analysis performed in the discriminant function, and in all cases, less than 40 percent of samples are identified to the correct stratigraphic level, which shows that the ability of discrimination between species based on their shape and morphology is poor. As sample sizes are small for many of the stratigraphic levels at Walou Cave, bootstrapped variance curves are not considered to be an appropriate method of analysis. On the basis of these results, there is no evidence suggesting identifiable evolution in morphological traits, gene flow or genetic drift within the Walou samples. Therefore H 6.3 cannot be rejected

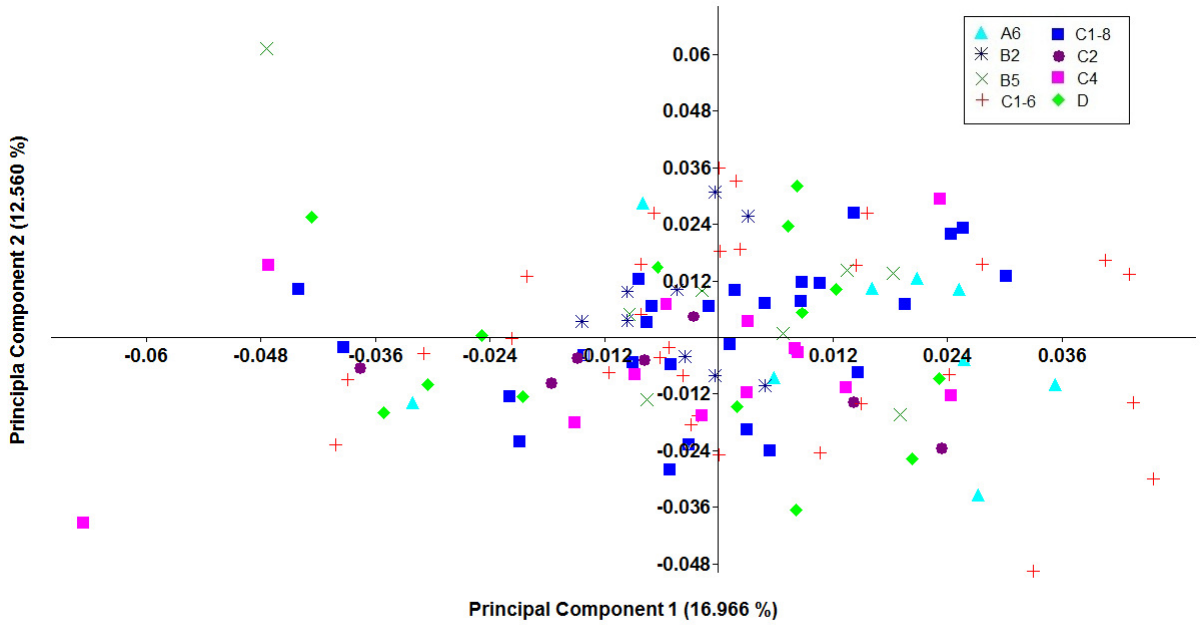

Figure 6.2: Results of Principle Component analysis showing major axis of variation in the Walou cave M. arvalis dataset on PC1 and PC2 by stratigraphic level.

PC	Eigenvalues	% Variance	Cumulative %
1	0.00043159	16.97	16.97
2	0.00031951	12.56	29.53
3	0.00030478	11.98	41.51
4	0.00020788	8.17	49.68
5	0.00016337	6.42	56.10
6	0.00014043	5.52	61.62
7	0.00010882	4.27	65.90
8	0.00009631	3.78	69.68
9	0.00008265	3.24	72.93
10	0.00007281	2.86	75.79

Table 6.6: *First 10 Eigenvalues for PC analysis of Walou Cave M. arvalis dataset including percentage of variation within the whole dataset explained by each PC and cumulative percentage.*

	A6	B1	B2	B5	C1-6	C1-8	C2	C
B1	**0.041939**							
	0.9951							
B2	**0.038669**	**0.048021**						
	0.9536	*0.9366*						
B5	**0.030115**	**0.03906**	**0.051386**					
	0.9995	*1*	*0.8305*					
C1-6	**0.019692**	**0.039582**	**0.039063**	**0.023974**				
	0.7572	*0.9116*	*0.8059*	*0.4681*				
C1-8	**0.024350**	**0.035309**	**0.038791**	**0.026807**	**0.01252**			
	0.8392	*0.9787*	*0.9461*	*0.9629*	*0.0658*			
C2	**0.030191**	**0.046374**	**0.037196**	**0.04017**	**0.028751**	**0.023329**		
	0.9960	*0.997*	*0.9703*	*0.9485*	*0.6545*	*0.9597*		
C4	**0.028176**	**0.037899**	**0.037379**	**0.03382**	**0.020833**	**0.01496**	**0.017862**	
	0.9775	*0.9991*	*0.9198*	*0.9742*	*0.9597*	*0.8155*	*1*	
D1	**0.027465**	**0.036989**	**0.042781**	**0.029176**	**0.018743**	**0.015733**	**0.028223**	**0.01**
	0.9843	*0.9989*	*0.8893*	*0.9156*	*0.4002*	*0.7991*	*0.9721*	*0.9*

Table 6.7: *Results of Discriminant Function analysis of Walou Cave M. arvalis by stratigraphic level. Procrustes distances are shown in bold and associated p-values in italics.*

	A6	B2	B5	C1-6	C1-8	C2	C4	D
A6	0.33333	0.26667	0.03333	0.13333	0.06667	0.03333	0.06667	0.06667
B2	0.18519	0.22222	0.11111	0	0.03704	0.18519	0.11111	0.14815
B5	0	0.5	0.125	0.25	0	0	0.125	0
C1-6	0.2	0	0.1	0.2	0.1	0.1	0.1	0.2
C1-8	0	0.28571	0.14286	0.14286	0.14286	0.14286	0.14286	0
C2	0.07143	0.14286	0.07143	0.14286	0	0.35714	0.07143	0.14286
C4	0.23077	0.07692	0.07692	0	0.07692	0.15385	0.38462	0
D	0	0.22222	0	0.11111	0	0.22222	0.11111	0.33333

Table 6.8: *Results of a cross-validation analysis of Walou Cave M. arvalis by stratigraphic level. Values are shown as proportion of samples from a sample assigned to each sample.*

6.3.4 HYPOTHESIS 6.4: THERE IS NO SIGNIFICANT DIFFERENCE IN INTRASPECIFIC VARIATION IN BOTH SIZE AND SHAPE OF *MICROTUS* LOWER M_1 THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT WALOU CAVE.

Hypotheses one and two have failed to show a significant difference in shape in the Microtine molars from many stratigraphic levels, however difference in size between the majority of levels is observed. In order to further investigate any small-scale patterns within the dataset, samples are analysed in Procrustes form space, to determine if better separation between levels can be gained when both centroid size and shape are taken into account. PCA is performed on Procrustes-fitted shape coordinates with log centroid size (as calculated during GPA) included.

Figure 6.3 shows the bivariate plot of PC1 and PCA, cumulatively accounting for 40. 83 % of the total size and shape variance in the sample. Complete Eigenvalues can be seen in table 6.9. No clear separation between groups can be seen on PC one and 2 or any other combination of PCs. To investigate any patterns within the data further, a discriminant function analysis with cross-validation is performed. Cross validation results are shown in table 6.10. As can be seen from the cross-validation results, the percentage of specimens assigned to the correct stratigraphic level is extremely low, <35% of specimens being assigned correctly, and all levels except C4 and C1-8 being assigned correctly < 15 percent of the time. In comparison with the cross-validation results gained from analysis of Procrustes-fitted coordinates where shape is removed (table 6.8) there is a significant reduction in correctly assigned specimens. This finding suggests that the ability to separate samples from different stratigraphic levels at

Walou Cave based upon their size and shape is extremely poor. The reduction of discriminant ability in comparison to Procrustes fitted samples suggests that the variation of size and shape are largely independent within this dataset and that the allometric component to morphological variation observed in hypothesis 6.1 has a negotiable effect. On the basis of the evidence above, hypothesis 6.4 cannot be rejected.

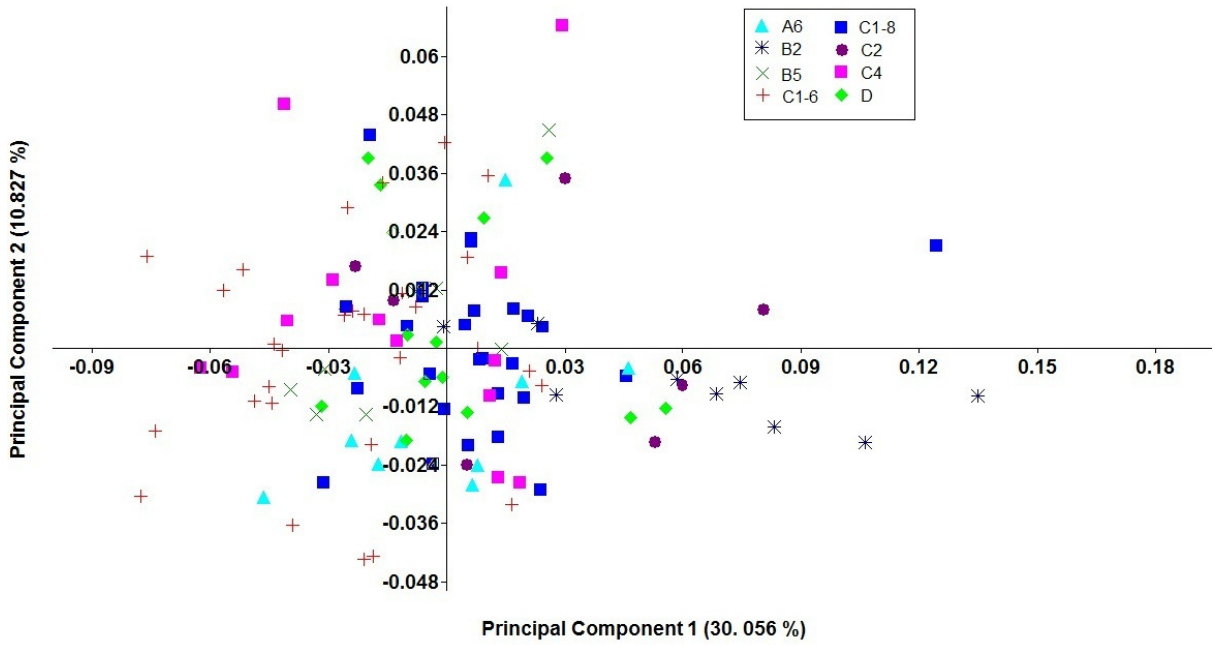

Figure 6.3 *: Results of Principle Component analysis in Procrustes form space showing major axis of variation in the Walou cave M. arvalis dataset on PC1 and PC2 by stratigraphic level.*

PC	Eigenvalues	% Variance	Cumulative %
1	0.001396	36.05	36.05
2	0.000419	10.82	46.88
3	0.000319	8.24	55.12
4	0.000271	6.99	62.11
5	0.000197	5.08	67.20
6	0.000162	4.17	71.38
7	0.00014	3.61	74.99
8	0.000109	2.82	77.81
9	0.000095	2.44	80.25
10	0.000083	2.14	82.40

Table 6.9: *Top 10 Eigenvalues for PC analysis in Procrustes form space of Walou Cave M. arvalis dataset including percentage of variation within the whole dataset explained by each PC and cumulative percentage.*

	A6	B2	B5	C1-6	C1-8	C2	C4	D
A6	0.125	0.06667	0.1	0.46667	0.16667	0	0.025	0.025
B2	0.03704	0.11111	0.07407	0.18519	0.22222	0.07407	0.11111	0.18519
B5	0.25	0	0.125	0.375	0.125	0	0.125	0
C1-6	0.1	0.2	0.2	0.1	0	0.1	0.1	0.2
C1-8	0	0.14286	0	0.14286	0.32857	0.14286	0	0.14286
C2	0.14286	0.14286	0.07143	0	0.21429	0	0.07143	0.35714
C4	0	0	0	0.07692	0.23077	0.07692	0.34154	0.15385
D	0	0.33333	0	0	0.22222	0.11111	0.11111	0.12222

Table 6.10: *Results of a cross-validation analysis of Walou Cave M. arvalis by stratigraphic level in Procrustes form-space. Values are shown as proportion of samples from a sample assigned to each sample.*

6.3.5 HYPOTHESIS 6.5: THERE IS NO SIGNIFICANT DIFFERENCE IN THE INTRASPECIFIC VARIATION OF SIZE IN *MICROTUS* LOWER M_1 TEETH AT WALOU CAVE CAUSED BY CLIMATE.

Previous research has identified an overall increase in the size of Microtine rodents in warmer conditions and a decrease in cooler conditions (Mc Guire, 2009; Montuire et al., 2004). In order to evaluate the statistical significance of change in size between climatic conditions at Walou cave, a Student's t-test is performed on the centroid sizes of *M. arvalis* to identify any systematic change in size according to climatic conditions.

Within each dataset, specimens from all cool stratigraphic levels are combined, as are those from all temperate and cool-temperate stratigraphic levels. Table 6.11 shows the results of the Student's t-tests including t-values and associated p-values to assess the significance of the mean sizes between climatic conditions. The resultant p-values show there is no significant difference in size between any climatic conditions. On the basis of these results, hypothesis 6.5 cannot be rejecte

	Cold	**Cool-Temperate**
Cool-Temperate	**0.287455165**	
	0.776042549	
Temperate	**0.558348054**	**0.717675087**
	0.579718951	*0.478164495*

Table 6.11: Results of Students t-test analysis of Walou Cave M. arvalis by climatic conditions. T-values are shown in bold and associated p-values in italics.

6.3.6 HYPOTHESIS 6.6: THERE IS NO SIGNIFICANT DIFFERENCE IN THE INTRASPECIFIC VARIATION OF SHAPE IN *MICROTUS* LOWER M_1 TEETH AT WALOU CAVE CAUSED BY CLIMATE.

In order to assess the degree of differentiation in the shape of the M_1 according to climatic conditions, a PCA is conducted on the Procrustes fitted data of *M. arvalis.*

Figure 6.4 shows the bivariate plot of PC 1 and PC 2, cumulatively accounting for 29.527

Percent of total variance (Complete Eigenvalues can be seen in table 6.10). It is clear these figures that there is no separation of the samples on PC1 and PC2. This remains true of further Principal components, with no separation between climatic groups observed on any combination of Principal Components. In order to further investigate any patterns of variation within the dataset according to climatic conditions, a discriminant function analysis with cross validation is performed (Tables 6.12 and 6.13 respectively). Discriminant function results show a significant difference in morphology between specimens from temperate and cool-temperate environments. However, cross-validation results suggest that although specimens are assigned to the correct climatic variable more frequently than to incorrect groups, correctly assigning specimens occurs < 40- 60 percent of the time, in all species. On the basis of these results, hypothesis 6.6 cannot be rejected.

	Cold	**Cool-Temperate**
Cool-Temperate	**0.02011678** *0.7677*	

Temperate	**0.01601229**	**0.01348571**
	0.0844	*0.026*

Table 6.12: *Results of Discriminant Function analysis of Walou Cave M. arvalis by climatic conditions. Procrustes distances are shown in bold and associated p-values in italics.*

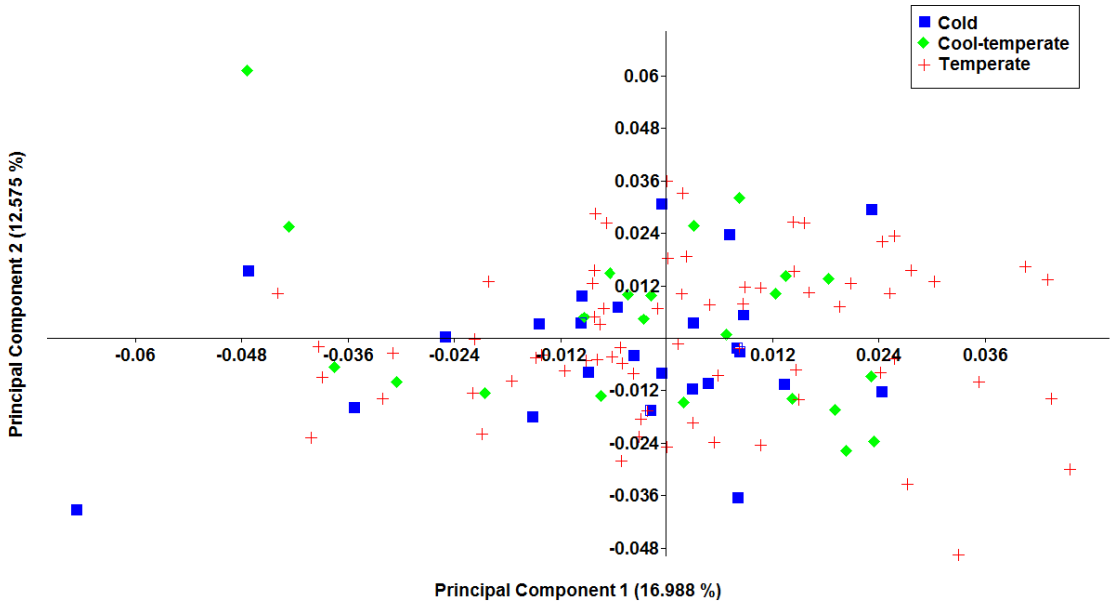

Figure 6.4: Results of Principle Component analysis showing major axis of variation in the Walou cave *M. arvalis* dataset on PC1 and PC2 by climatic conditions.

	Temperate	**Cold**	**Cool-temperate**
Temperate	0.5634	0.2535	0.1831
Cold	0.32	0.4	0.28
Cool-temperate	0.3182	0.2727	0.4091

Table 6.13: *Results of a cross-validation analysis of Walou Cave M. arvalis by climatic conditions. Values are shown as proportion of samples from a sample assigned to each sample.*

6.4 DISCUSSION

The highly variable morphology of *Microtus* M_1 teeth has been remarked upon by many authors (e.g.; Chaline, 1989., Van der Meulen, 1964). However, there has been little attempt to identify the factors that have an effect upon morphological change through time. The well-dated and well understood Walou Cave sequence has provided an opportunity to apply the information gained from chapter 4 and assess the variance in M_1 morphology in archaeological datasets. This chapter has attempted to address the effect of climate and time upon the morphology of the Walou cave *Microtus* populations and several conclusions can be drawn from the data presented above.

Separation of *M. arvalis* and *M. agrestis* samples is determined using a discriminant function based upon modern material. There are inherent difficulties associated with attempting to investigate the taxonomy of ancient material, as often DNA analysis is not possible due to degradation of organic matter within remains. These problems were also present within this study, where a GMM methodology built on modern material of known species/ origin is then applied to archaeological material to separate *M. agrestis* and *M. arvalis* specimens. In doing so, an assumption is made that the modern and archaeological M_1 morphology, whilst evolving over time, has remained similar enough within species to remain identifiable as that species. As Microtine rodents are known to have extremely plastic and variable teeth and to evolve extremely rapidly, the validity of applying discriminant functions built on modern material, in particular to the early Middle Pleistocene could be questioned.

In order to provide the most robust samples for statistical analysis, the modern samples were chosen in order to capture the widest possible geographical range of specimens, with the aim of capturing as much of the variance in morphology seen within the specie as possible. Even with this wide range of variation, PCA and discriminant function analyses were able to discriminate between all species with an extremely high degree of statistical significance, even in the case of *M. agrestis* and *M. arvalis*, which have extremely similar morphological characteristics. This finding suggests that the GMM methodology provides an extremely robust method for identifying *Microtus* species based on M_1 morphology.

Although identifying species based on morphological characteristics of hard tissues will always prove problematic, with the possibility of divergent evolution creating 2 unrelated species with similar morphological characteristics, it is a standard practice within palaeontology and taxonomy. The author would argue that the use of a discriminant function based on modern samples to separate archaeological material is an extension of this practice- indeed, all specimens, and modern and archaeological within this study were identified using morphological characteristics.

However, it should be borne in mind that 'species' as they are identified in ancient material, may not represent the direct evolutionary lineage of the modern species which share the same name. Regardless, it is clear from the results gained, that there are two distinct morphological samples present in the Walou material, and to draw the conclusion they represent separate species, most likely part of the *M. arvalis/ M. agrestis* lineages, based upon their similarity to modern material.

In the Walou cave dataset, there appears to be a variable amount of allometry present in different species. As with the modern samples in chapter 4, the majority of variance in shape within each dataset is not explained by Allometry. *M. agrestis* and *M. gregalis* samples show insignificant allometric influence, possibly as a result of small sample sizes (25 and 10 specimens respectively). The larger *M. arvalis* dataset (116 specimens) show a statistically significant (p= 0.0004) allometric component to the dataset, with 2.79 percent of the variance in shape in the dataset being explained by variation in size. The percentage of allometry within the Walou Cave *M. arvalis* dataset is lower than that observed within the similar sized modern dataset in chapter 4 (4.43 percent). This is what would have been predicted, based upon the fact that it is known that *Microtus* morphology and body size are known to vary in response to both genetic and environmental factors (Schweizer et al., 2007). As *Microtus* populations are known to have a high degree of inter-population genetic and morphological variance (Jaarola et al., 2004) and that the modern dataset covers a wide geographical range of distinct populations, it follows that we would expect the allometric effect to be larger in this dataset.

The overall impact of the allometric component to the *M. arvalis* dataset is considered to be small enough not to require removal prior to further analyses. This assumption is confirmed by the reduced ability of a cross-validation to distinguish between samples in Procrustes form-space in comparison to standard shape space, where the size component is removed (hypothesis 6.4).

The results of a Students' t-test show that there is a statistically significant difference in size between most stratigraphic levels. This difference in size does not appear to increase as the samples become younger in age, as would be predicted by Cope's rule,

which states that population lineages tend to increase in body size over evolutionary time due to increased evolutionary fitness (Cope, 1871). However, as Hone & Benton (2005) and Gould (1997) suggest, this generalised rule is not true of all species. The observed fluctuation in size through the Walou cave sequence also does not appear to be a factor of climate, as both when analysed on a stratigraphic-level scale (hypothesis 6.2) and when all specimens from specific climatic conditions are combined (hypothesis 6.5), no significant increase or decrease in size is observed. This result is in opposition to Bergman's Rule (Bergman, 1847) which states that individuals living in cold climatic conditions will increase in size to reduce their body mass to surface area ratio and therefore become more thermally efficient. However, it is also in opposition to the findings of Nadachowski (1984) and Mointure & Brunet-Lecomte (2004) who found that *Microtus* living in colder conditions are smaller than those in warm habitats. The lack of differentiation in size at Walou cave may be explained by the species being studied; modern *M. arvalis* is found over a wide range of habitats and climatic conditions ranging from temperate forest to steppic environments (Gromov & Polyakov, 1992), suggesting it has a wide climatic tolerance, which may reduce the selective pressure towards larger or smaller body size. There is a significant difference in morphology observed between samples from temperate and cool-temperate conditions, although poor cross-validation results suggest that the variation in morphology between these two groups is not well-defined.

Overall, throughout the stratigraphic sequence at Walou Cave, very little variance in morphology is observed (the results of discriminant function analysis show that $p>0.8$ for the ability to discriminant between stratigraphic levels in all cases). Cross-validation results also show that less than 40 percent of specimens are assigned to the correct

stratigraphic level in all cases. The cause of the homogeneity of the sample is not clear, as *Microtus* species are known to evolve extremely rapidly and the morphology of their teeth is known to be extremely plastic (Gutherie, 1965). As the Walou Cave stratigraphic sequence is known to span approximately 90,000 years, it would be expected that an observable amount of morphological variation would have occurred. It has also been demonstrated in chapter 5 that there is a very large amount of inter- and intra-specific genetic variation in modern populations of *Microtus*, which is also reflected in the morphology of the M_1. Therefore, it is possible that the lack of distinction between samples at Boxgrove is likely to be a factor of the small available sample size, or that the *M. arvalis* population at Walou cave is static, with very little genetic mixing with other populations throughout the last 90,000 years.

6.5 CONCLUSIONS

- The *M. arvalis* population displays a fluctuating M_1 size throughout the stratigraphic sequence, which does not appear to be a factor of either morphological change, evolutionary pressure towards an increase in size, or climate.

- The morphology of the M_1 shows very little variation throughout the stratigraphic sequence and does not appear to be affected by climatic conditions, evolutionary or genetic change through time.

CHAPTER 7
CASE STUDY 2- BOXGROVE

7.1 INTRODUCTION

Chapter 4 identified patterns of morphological variation in modern material and chapter 5 further investigated the range of morphological variation found in archaeological material from Walou Cave. This chapter attempts to explore further the effects of environmental factors and evolutionary changes in the morphology of the *Microtus* lower M_1 in a dataset of archaeological material from the site of Boxgrove, West Sussex, in comparison to the modern and Walou cave datasets discussed in chapters 4 and 5.

Boxgrove is an extremely important site within the British and European Palaeolithic. Several climatic episodes are evident within the stratigraphic sequence at the site, which comprises a well preserved landscape dating to approximately 500 Kya. The size of the preserved area (of which only a fraction has been excavated) along with the

numerous flint artefacts (some *in situ*) and mammalian remains (including cut-marked bone) are extremely unusual for a site of this age (Roberts & Parfitt, 1999). The well-preserved stratigraphic sequence and faunal remains at the site provide excellent proxies to interpret environmental and climatic change; these have already been discussed at depth in Chapter 2

As the stratigraphic sequence at Boxgrove is well understood and the recovery of remains so thorough, the *Microtus* specimens from the site are assumed to be well provenanced and from known climatic and stratigraphic unit (See section 7.2 for further details).

The diversity of *Microtus* remains, and the rapid evolution and divergence displayed by the genus, are well documented (e.g., Guthrie, 1965*;* Chaline *et al.*, 1999). It has been demonstrated that the *Microtus* dentition is plastic and susceptible to changes in shape due to epigenetic factors, although genetic factors play a much greater role in determining molar shape (Uhlikova, 2004), as discussed in chapter 5. However, it is only relatively recently, with the rise of powerful statistical techniques, that attempts to understand the various factors affecting the morphology of *Microtus* teeth have been possible. As the teeth of *Microtus* and other Arvicoline rodents are known to have such high inter- and intra-specific variability (Repenning *et al.*, 1990), investigating the amount to which both genetic and environmental factors affect tooth morphology of these species is of interest.

The present chapter will assess the degree to which temporal and environmental factors determine the patterns of morphological diversity in *Microtus at* Boxgrove by examining the following main aims:

1) **Evaluation of the effect of size on the shape of *Microtus* M_1 teeth.**

As discussed in chapter 1, allometry is of interest to this study, in particular, static allometry, which describes the relationship of size and shape in adult individuals. It is important to assess the degree of allometry present within the M_1 of the *Microtus* species included within this study, as if a large allometric component is found within the data; it may thus be desirable to remove this before subsequent analyses (e.g. Penin *et al*., 2002; Frost *et al*., 2003; Mitteroecker *et al*., 2004).

Both the Modern and Walou cave datasets (analysed in chapters 4 and 5 of this study) have demonstrated statistically significant allometric components within the species datasets, in most cases accounting for c. 5% of the variance observed within PC1. Both of these datasets include samples from a wide range (geographically in the case of modern material and temporally in the case of Walou Cave). The samples from Boxgrove are significantly more constrained, temporally and geographically as they contain samples from a single site over a relatively short period of time. Therefore, the relative proportions of allometry displayed in Boxgrove samples may be of interest in comparison with the Walou Cave and Modern datasets.

Therefore, the following hypothesis is erected;

Hypothesis 7.1- *There is no significant allometric component to intraspecific diversity in Microtus lower M_1 morphology at Boxgrove.*

If an allometric component is found within the Boxgrove datasets, further analyses will be performed in order to investigate the reasons for variance in both size and shape at Boxgrove;

2) **Evaluation of the degree of morphological change present through the stratigraphic sequence at Boxgrove.**

As discussed in detail within chapter 1, *Microtus* species are known to have evolved extremely rapidly, and this evolution is reflected in their dental morphology (Chaline *et al.*, 1999). This provides the potential for dental morphology in *Microtus* species to be used as a relative dating method of sediments. However, this is an area which has not been studied in any detail in *Microtus* species, unlike in other closely related Microtine rodents such as *Arvicola*/ *Mimomys* (Von Kolfschoten & Van Koeningswald, 1996; Von Kolfschoten, 1990).

Evidence of morphological change, in terms of shape or size, throughout the sequence may represent rapid evolution within a single population, population dispersal or replacement. As the time period represented by the *Microtus* remains from the Boxgrove sediments is thought to be relatively short, representing part of a single interglacial cycle, it may be expected that there will be little or no morphological evolution through the sequence. Rapid diversification and evolution of distinct M_1 morphologies have been identified within separate populations of *Microtus* in the Orkney Isles. This rapid differentiation of populations occurred from the initial introduction of *Microtus* to the islands in the Neolithic to the present day, suggesting the possibility of rapid morphological change in *Microtus* species over short time-frames (Corbet, 1986). However, a generalised model of the rate of dental evolution in *Microtus* species has not, to date, been studied.

In order to investigate morphological change at Boxgrove, the following hypotheses are erected:

Hypothesis 7.2*: There is no significant intra-specific variation in Microtus lower M_1 tooth size caused throughout the stratigraphic sequence at Boxgrove.*

The size of *Microtus* M_1 teeth throughout the stratigraphic sequence at Boxgrove will be analysed for each species separately.

Hypothesis 7.3*: There is no significant intra-specific variation in Microtus lower M_1 tooth shape caused throughout the stratigraphic sequence at Boxgrove.*

The variance in shape throughout the stratigraphic sequence at Boxgrove will be analysed for each species individually.

If hypotheses 7.2 and 7.3 show no clear indication of morphological evolution or change in size through the stratigraphic sequence, the co-variance of both size and shape throughout the sequence will be examined in Procrustes Form Space;

Hypothesis 7.4: *There is no significant difference in intraspecific variation in both size and shape of Microtus lower M_1 throughout the stratigraphic sequence at Boxgrove.*

If there is no clear evolutionary explanation for the variance in *Microtus* morphology throughout the stratigraphic sequence at Boxgrove, the effect of climate upon shape and size of the M_1 of each species of *Microtus* will also be investigated individually;

3) Evaluation of the effect of external environmental factors, such as prevailing climate on the morphology of the *Microtus* M_1.

An alternative explanation for morphological change in shape or size of *Microtus* teeth through the stratigraphic sequence at Boxgrove is the influence of climatic factors

upon epigenetic variation. Several studies have shown that *Microtus* teeth display a relatively low degree of epigenetic variation (Uhlikova, 2004). However, distinct morphological changes in the morphology of *Microtus* dentition attributed to climatic change have been demonstrated in more than one study (Mc Guire, 2009; Montuire *et al.*, 2004). *Microtus* species have also been shown to increase in size in warmer conditions and decrease in cooler ones, the opposite of what might be predicted by Bergmans' Rule (Bergman, 1847) . Therefore, it is possible that the size of *Microtus* teeth may also change in line with general body-size change in response to the prevailing climatic conditions.

The climatic conditions for each stratigraphic level at Boxgrove are well understood, and the sequence records a decline from wooded, vegetation-rich temperate conditions into cool, open and arid conditions (Roberts & Parfitt, 1999) over a relatively short space of time. Therefore, it may be possible to identify specific morphological changes or changes in size which are associated with climatic conditions in *Microtus* species.

On the basis of the literature and discussion cited above, the following hypotheses are erected:

Hypothesis 7.5: *There is no significant difference in the intraspecific variation of size in Microtus lower M_1 teeth at Boxgrove caused by climate.*

Hypothesis 7.6: *There is no significant difference in the intraspecific variation of shape in Microtus lower M_1 teeth at Boxgrove caused by climate.*

7.2 MATERIAL AND METHODS

The material used within all Boxgrove analyses and a summary of the methods of analysis used are provided below;

7.2.1 MATERIAL

A sample of 136 specimens representing the entire collection of undamaged specimens of *Microtus* from Boxgrove is used in this chapter. Table 7.1 shows identifiable remains (TIR) recovered from the site and the corresponding minimum number of individuals (MNI).

Large concentrations of small mammal remains are usually found in locations where they have been accumulated by birds of prey (roosting sites in caves etc) or in dens of other small carnivores (Andrews, 1990). As Boxgrove is an open-air site, birds of prey would probably have roosted elsewhere in the local environment (possibly the forested down land block above the site, as shown by faunal remains recovered from the site) and large accumulations of micromammal remains were not recovered from the site (Roberts, 1999b). Rather, the Boxgrove microfaunal remains have been recovered as part of an intensive sieving programme, as described in Parfitt (1986). Recovery was hampered by the fragile nature of the bones, which had been distorted due to sediment compaction. Bulk sieving of the sediment samples also caused considerable damage to teeth and bones (Parfitt, 1986). Breakage and damage to the teeth is extremely common in the samples examined for inclusion within this study. In

particular, many specimens have damage to T1-T5 as well as the AC region of the tooth. Therefore, the number of specimens suitable for analysis is greatly reduced in comparison with the number of identifiable specimens (table 7.1). Total numbers of individuals used in this chapter and their corresponding stratigraphic levels are shown below in table 7.2.

	TFI	MNI
M. agrestis/ arvalis	390	235
M. gregalis	41	29
M. subterraneus	390	219

***Table 7.1**: Total number of recovered identifiable specimens (TFI) and Minimum Number of Individuals (MNI) combined for all stratigraphic levels at Boxgrove. (Modified from Parfitt, 2000)*

	3	**4a**	**4b**	**4c**	**4d**	**5a**	**5b**	**6**
M. agrestis/ arvalis	5	0	1	52	0	10	7	16
M. gregalis		0	0	4	0	0	0	0
M. subterraneus	3	0	0	27	0	6	2	3

***Table 7.2:** Number of individuals suitable for GMM analysis per stratigraphic level at Boxgrove.*

Several analyses in the chapter separate the datasets according to the prevailing climatic conditions at the time the sediments were deposited within each stratigraphic level. Climatic reconstructions have been calculated using the Taxonomic Habitat index

and are taken from Roberts & Parfitt (1999). Within these analyses, all samples from each climatic variable are amalgamated into single datasets. Climatic conditions for each stratigraphic level are shown in table 7.3.

Stratigraphic Level	Climate
3	Cool
4a	Temperate
4b	Temperate
4c	Temperate
5a	Temperate
5b	Cool
6	Cool

Table 7.3: *Climatic conditions reconstructed for each stratigraphic level at Boxgrove (as calculated in Roberts & Parfitt, 1999).*

7.2.2 METHODS

The sample from Boxgrove contains material catalogued as *M. arvalis*/ *agrestis* on the basis of M_1 morphology, which is usually considered too similar to separate the two species. As shown in chapter 5, a discriminant function based on known modern material can be used to assigning unknown archaeological specimens to *M. arvalis* or *M. agrestis*, and has been demonstrated to be a reliable method for separating modern material of the two species.

Therefore, prior to any analysis , discriminant functions are generated from modern *M. agrestis*, *M. arvalis*, *M. gregalis* and *M. subterraneus,* as discussed in chapter 4 (discriminant functions separating known species in the modern dataset p <0.0001). The combined M.*arvalis*/ *agrestis* Boxgrove sample is then assigned to species on the basis of the modern discriminant function, with each specimen treated as an unknown. All specimens within the M.*arvalis*/ *agrestis* sample are assigned to either *M. arvalis* or *M. agrestis*, with no specimens assigned to *M. subterraneus* or *M. gregalis*, suggesting that the discriminant function remains very statistically robust when applied to archaeological material, as seen in the Walou Cave dataset in Chapter 6. Results from this discriminant function assignation can be seen in Appendix B. A summary of the species and specimen numbers at Boxgrove, including the *M*. *arvalis*/ *agrestis* samples separated by the discriminant function, is shown in Table 7.4

As shown in table 7.4, few *M. arvalis* and *M. gregalis* suitable for GMM analysis are recovered from Boxgrove. Therefore only *M. agrestis* and *M. subterraneus* are used in testing hypotheses H2-H5.

	3	**4a**	**4b**	**4c**	**4d**	**5a**	**5b**	**6**
M. agrestis	2	0	1	25	0	4	5	13
M. arvalis	0	0	3	12	0	0	0	3
M. gregalis	0	0	0	4	0	0	0	0
M. subterraneus	3	0	0	27	0	6	2	3

Table 7.4: *Number of individuals per species and stratigraphic level at Boxgrove after use of discriminant function analysis to assign M. arvalis and M. agrestis to species.*

Twenty-five landmarks are collected from each tooth, as described in chapter 3, comprising 15 fixed landmarks and 10 semi-sliding landmarks along the curve of the AC region. In all analyses, landmarks are firstly superimposed using Generalised

Procrustes Analysis (GPA) to remove variation due to translation and rotation and to separate shape from size.

When looking at the difference in morphology between stratigraphic levels at Boxgrove, *M. agrestis* and *M. subterraneus* are chosen as the only species suitable for this analysis. The reason for this selection is that *M. arvalis and M. gregalis* are present in only very small numbers at Boxgrove and therefore statistical analyses are not reliable as the sample sizes are too small and do not cover a sufficient stratigraphic range .

H 7.1: A multivariate regression of centroid size on Procrustes-fitted shape coordinates is performed in order to quantify the effect of shape upon size within the dataset.

H 7.2 and 7.5: A Students' t-test is performed on the centroid sizes of each sample, as calculated during the Procrustes fit of the combined samples.

H 7.3 and 7.6: Principal Components Analysis (PCA) are performed using the Procrustes-fitted coordinates from the GPA to visualise the major axes of variation in the dataset. In order to investigate the variation within the datasets further, a discriminant function with cross-validation is then performed using the Mahalanobis D^2 distances between group means. A range of variance values is then calculated via bootstrapping the original data 1000 times. The bootstrap value are then plotted to provide curves illustrating the distribution of variance in shape-space for each sample.

H7.5: Where variation within the dataset is suspected to be caused by both size and shape, analyses are performed in Procrustes form-space. Log centroid size (as calculated during GPA) is added to Procrustes fitted shape co-ordinates. Principle

component analyses are performed on the combined dataset to visualise the major axis of variation within the sample. Discriminant function analyses are used to quantify the separation between groups and the strength of the discriminant function analysis is assessed using leave-one out cross-validation.

7.3: RESULTS

Summaries of all results gained from the Boxgrove sample are presented below, according to hypothesis.

7.3.1 THERE IS NO SIGNIFICANT ALLOMETRIC COMPONENT TO INTRASPECIFIC DIVERSITY IN *MICROTUS* LOWER M_1 MORPHOLOGY AT BOXGROVE.

Multivariate regression of Procrustes co-ordinates onto centroid size is performed for each species in order to summarise any relationship between the size and morphology of the M_1. Full centroid sizes for all individuals are provided in appendix C. The results, as shown in Table 7.5, suggest that allometry explains only a minimal amount (> 5%) of the morphological variance within any single *Microtus* species at Boxgrove. The resulting p-values show that allometry can be considered to be statistically insignificant at 95% confidence within each species dataset. Therefore, Hypothesis 7.1 cannot be rejected.

	Total % predicted	p-value
M. arvalis	4.539	0.3326
M. agrestis	2.4715	0.2731
M. subterraneus	4.9138	0.398

Table 7.5 *: Total percentage of predicted morphological change explained by allometry per dataset and associated p-values resulting from regression of centroid size against Procrustes co-ordinates.*

7.3.2 HYPOTHESIS 7.2: THERE IS NO SIGNIFICANT INTRA-SPECIFIC VARIATION IN *MICROTUS* LOWER M_1 TOOTH SIZE CAUSED THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT BOXGROVE.

Centroid size is used to examine intraspecific changes in size through the stratigraphic sequence (Tables 7.6 for *M. agrestis* and 7.8 for *M. subterraneus*). Within each species, the centroid size of specimens from each stratigraphic level is compared to those from every other stratigraphic level, using Student's t-tests.

The number of stratigraphic levels suitable for inclusion within this analysis is reduced due to the small number of samples available per stratigraphic level in some species. In the *M. agrestis* dataset, level 3 contained 3 specimens only and in the *M. subterraneus* dataset, levels 3, 4b and 5b contained 3, 2 and 2 specimens respectively and, therefore, these levels are excluded from the analyses due to insufficient sample size.

Tables 7.7 and 7.9 show the t-values (italics) and corresponding p-values (bold) from a Student's t-test analysis performed on the centroid sizes of the landmarked specimens. These results show there is no statistically significant difference in size for either species between any of the stratigraphic levels. Therefore, hypothesis 7.3 cannot be rejected on the basis of the results of this analysis and no evidence of size change due to evolutionary selective pressure or genetic change over time throughout the stratigraphic sequence is suggested.

Stratigraphic Level			
4c	5a	5b	6
1912.2892	2419.6615	2435.8317	2314.6534
2295.5136	2560.2934	2366.7195	2385.6160
2235.4795	2555.0143	2341.5890	2315.3756
2534.8874	2276.9265	2263.6709	2626.6684
2748.9606	2405.8079	2145.7042	2465.8294
2335.0064	2555.0143		2403.6556
1757.3501	2276.9265		2328.3943
2256.1580			2551.9028
2334.0624			2300.6601
2017.3921			2396.1511
2538.2124			2386.8670
2270.6760			
2361.7136			
2272.3189			
2283.9532			
2259.6964			
2327.6043			
2407.0901			
2635.2228			
2816.1748			
2082.2361			
2433.5079			
1907.3563			

Table 7.6 *: Boxgrove M. agrestis centroid sizes by stratigraphic level.*

	4c	5a	5b	6
5a	**-1.27933**			

	0.211282		
5b	**-0.04504**	**1.773809**	
	0.964418	*0.106492*	
6	**-1.2293**	**0.556101**	**-1.64848**
	0.227921	*0.585836*	*0.121505*

***Table 7.7**: Results of Students t-test on M. agrestis dataset. T-values are shown in bold and p-values in italics.*

Stratigraphic level		
4c	**5a**	**6**
1960.0215	2039.1067	2222.4570
2055.4011	2118.1458	2271.6495
1997.0357	2117.0404	2150.8777
2012.3803	2209.8882	2275.8123
2424.2299	2184.6574	2061.3627
2410.3316	2205.6701	
2315.3611		
2128.2384		
2545.3728		
2040.7938		
2035.5960		
2645.7582		
2219.1750		
2233.1756		
2114.8440		
2077.2957		
2108.8612		
1934.7267		
2055.6021		
2134.4218		
2086.7552		
2159.9989		
2026.5833		
2151.9282		
2076.3582		

***Table 7.8**: Boxgrove M. subterraneus centroid sizes, as calculated during GPA by stratigraphic level*

	4c	**5a**	**6**

5a	**0.161743**	
	0.87263	
6	**-0.45919**	**-1.06936**
	0.649641	*0.312748*

Table 7.9: *Results of Students t-test on the Boxgrove M. subterraneus dataset. T-values are shown in bold and p-values in italics*

7.3.3- HYPOTHESIS 7.3: THERE IS NO SIGNIFICANT INTRA-SPECIFIC VARIATION IN *MICROTUS* LOWER M_1 TOOTH SHAPE CAUSED THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT BOXGROVE.

In order to assess the degree of differentiation in the shape of the M_1 within species through the stratigraphic sequence, PCA is conducted on the Procrustes-fitted data of *M. agrestis* and *M. subterraneus* samples. *M. arvalis* samples are excluded from this analysis due to the extremely small sample sizes per stratigraphic level.

Figures 7.1 and 7.2 show the bivariate plots of PC's 1 and 2 for *M. agrestis* and *M. subterraneus*, cumulatively accounting for 31.725 and 40.064 percent of total variance respectively (complete eigenvalues for both species can be seen in table 7.10). It is evident from looking at both of these figures that there is no separation of the samples on PC1 and PC2. This remains true of further Principal components for both *Microtus* species, with no separation between stratigraphic groups observed on any Principal Component. In both species, the amounts of variance described on PC 1 and PC2 are very similar in size and, when compared to the PC values of the Modern and Walou

cave datasets, also explain a relatively small amount of the variance within the dataset. These results suggest there is very little systematic change throughout the dataset.

Tables 7.11 and 7.12 show the results of discriminant function analyses by stratigraphic levels for *M. agrestis* and *M. subterraneus* respectively. No significant pattern of variation is found in the morphology of the lower first molar between the stratigraphic levels at Boxgrove. Tables 7.13 and 7.14 show Cross-validation results. The ability to assign specimens to the correct sample is extremely poor (< 20 % in all cases). Samples which are more temporally distant (i.e. units 3 and 6) do not show a greater Procrustes distance between samples than those which have smaller temporal separation (i.e. units 4b and 4c) . There is no evidence suggesting identifiable evolution in morphological traits, gene flow or genetic drift within the Boxgrove samples. Therefore H 7.3 cannot be rejected

PC	Eigenvalues	% Variance	Cumulative %
1	0.0005061	17.29	17.29
2	0.0003930	13.13	30.42
3	0.0003172	10.04	40.46
4	0.0002872	9.81	50.27
5	0.0002234	7.53	57.80
6	0.0001813	6.19	63.99
7	0.0001515	5.17	69.16
8	0.0001065	3.54	72.70
9	0.0001505	2.91	75.61
10	0.0000808	2.76	78.37

PC	Eigenvalues	% Variance	Cumulative %
1	0.0005157	22.50	22.50
2	0.0001303	17.55	40.05
3	0.0003431	12.54	52.59
4	0.0002212	8.08	60.67
5	0.0001703	6.22	66.89
6	0.0001300	4.75	71.64
7	0.0001139	4.15	75.79
8	0.0000001	3.15	78.94
9	0.0000001	2.96	81.90
10	0.0000001	2.78	84.68

Table 7.10: *First 10 Eigenvalues for PC analysis of Boxgrove M. agrestis (left) and M. subterraneus (right) datasets including percentage of variation within the whole dataset explained by each PC and cumulative percentage.*

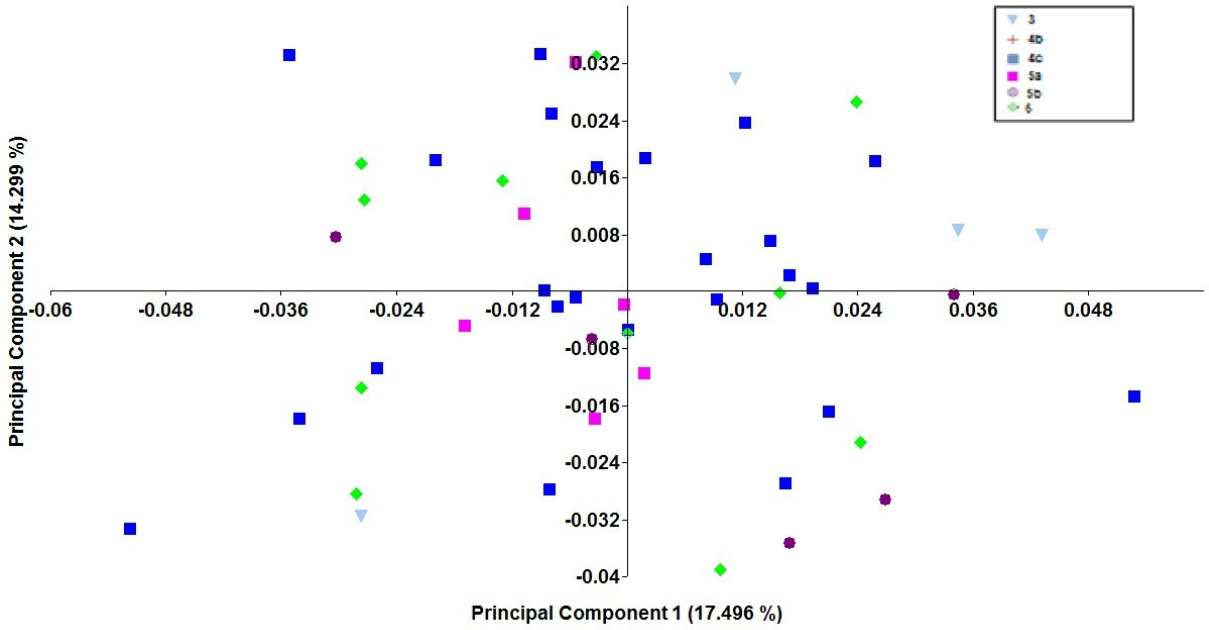

Figure 7.1: *Results of Principle Component analysis showing major axis of variation in the Boxgrove M. agrestis dataset on PC1 and PC2 by stratigraphic level*

	3	4b	4c	5a	5b
4b	**0.050072**				
	0.9951				
4c	**0.034153**	**0.036152**			
	0.9982	*0.9911*			
5a	**0.051941**	**0.047272**	**0.032637**		
	0.9438	*0.9693*	*0.9918*		
5b	**0.038318**	**0.044764**	**0.035382**	**0.053691**	
	0.9867	*0.9862*	*0.9602*	*0.9752*	
6	**0.03044**	**0.039825**	**0.018122**	**0.034019**	**0.032773**
	0.9999	*0.9805*	*0.9851*	*0.9926*	*0.9874*

Table 7.11: *Results of Discriminant Function analysis of Boxgrove M. agrestis by stratigraphic level. Procrustes distances are shown in bold and associated p-values in italics.*

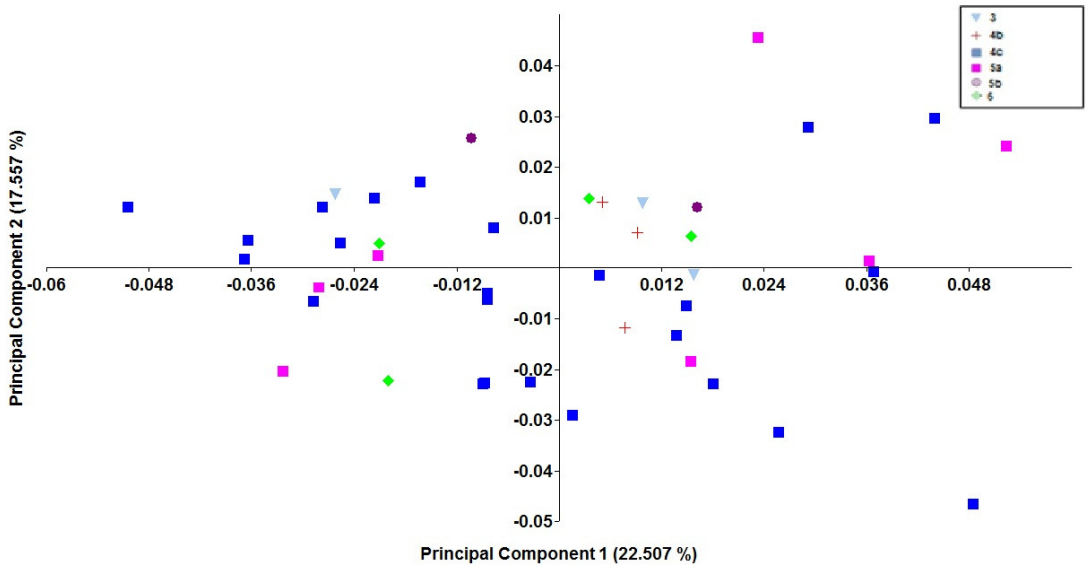

Figure 7.2: *Results of Principle Component analysis showing major axis of variation in the Boxgrove M. subterraneus dataset on PC1 and PC2 by stratigraphic level.*

	3	4b	4c	5a	5b
4b	**0.042657**				
	0.8927				
4c	**0.032389**	**0.026371**			
	0.9983	*0.9979*			
5a	**0.035413**	**0.030941**	**0.024468**		
	0.9876	*0.9970*	*0.9956*		
5b	**0.03625**	**0.047571**	**0.038581**	**0.046227**	
	0.9938	*0.9448*	*0.9867*	*0.9882*	
6	**0.033515**	**0.046645**	**0.029773**	**0.039359**	**0.042183**
	0.9651	*0.8541*	*0.9999*	*0.9685*	*0.9466*

Table 7.12: *Results of Discriminant Function analysis of Boxgrove M. subterraneus by stratigraphic level. Procrustes distances are shown in bold and associated p-values in italics.*

	3	**4b**	**4c**	**5a**	**5b**	**6**
3	0.000	0.333	0.333	0.000	0.000	0.333
4b	0.000	0.000	0.000	0.500	0.000	0.500
4c	0.200	0.150	0.200	0.100	0.200	0.150
5a	0.000	0.286	0.429	0.143	0.000	0.143
5b	0.000	0.400	0.200	0.200	0.200	0.000
6	0.182	0.182	0.273	0.091	0.091	0.182

Table 7.13: *Results of a cross-validation analysis of Boxgrove M. agrestis by stratigraphic level. Values are shown as proportion of specimens from the total number in that sample assigned to each level.*

	4b	**4c**	**5a**	**5b**	**6**
4b	0.333	0.000	0.333	0.333	0.000
4c	0.333	0.208	0.250	0.083	0.125
5a	0.333	0.333	0.167	0.000	0.167
5b	0.333	0.333	0.333	0.000	0.000
6	0.286	0.143	0.286	0.143	0.143

Table 7.14: *Results of a cross-validation analysis of Boxgrove M. subterraneus by stratigraphic level. Values are shown as proportion of specimens from the total number in that sample assigned to each level*

In order to investigate further any morphological differences within the Boxgrove *M. agrestis* dataset, the amount of variance in M_1 shape in each stratigraphic level is investigated. Variance values are calculated from Procrustes-fitted landmark co-ordinates and then a bootstrap analysis are repeated one thousand times. The Bootstrapped results for each variance figure are then plotted to produce a variance curve, as shown in figure 7.3. Sample sizes for *M. subterraneus* are considered too small for analysis using this method.

In level 5a, the original variance value and distribution curve is clearly reduced in comparison with the other levels, in which a similar amount of variance is observed. Due to the small sample sizes within this dataset, it is possible that this result is an artefact of small sample sizes. Level 5a is a temperate level and, therefore, it would be expected that an increased amount of morphological variance would be observed in comparison with samples from cold climatic conditions (levels 5b and 6).

On the basis of the information presented above, no discernable difference in the morphology of the M_1 has been observed within the Boxgrove sample. The morphology of samples throughout the stratigraphic sequence appears to be extremely homogenous. Therefore, hypothesis 7.3 cannot be rejected.

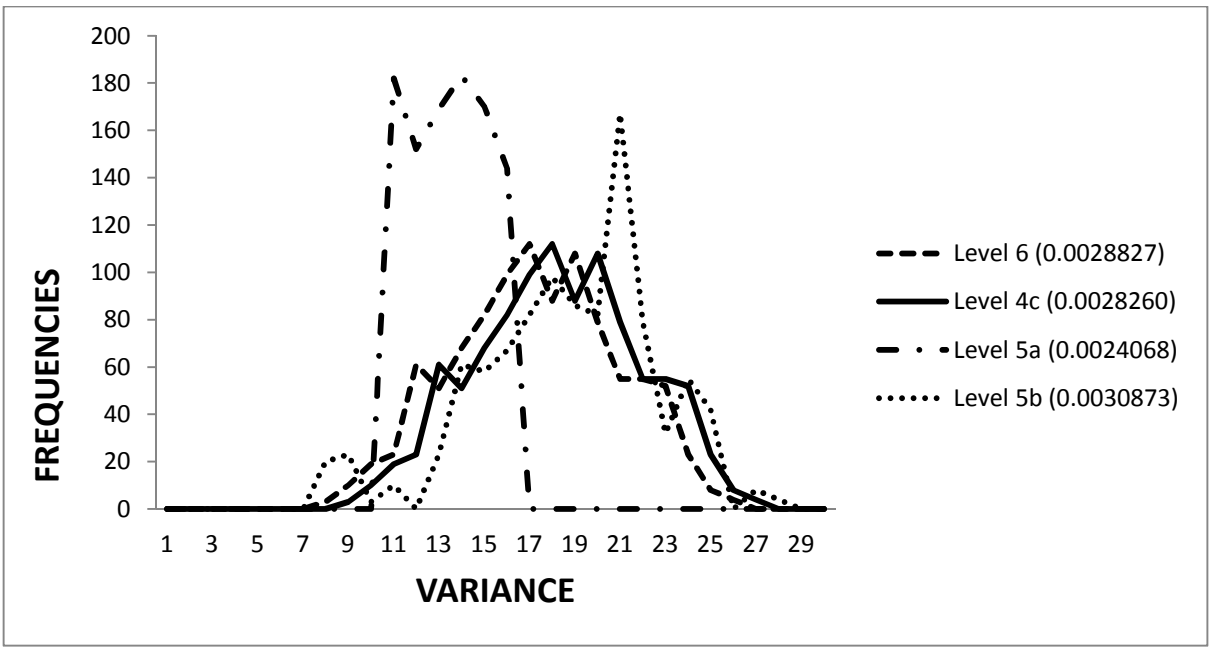

Figure 7.3: Variances in shape space for M. agrestis at each stratigraphic level and their bootstrap distributions. Bootstrap distributions for the shape variances of the 5 different groups (1000 bootstraps each; colour coding shown in key followed by original variance value).

7.3.4 HYPOTHESIS 7.4: THERE IS NO SIGNIFICANT DIFFERENCE IN INTRASPECIFIC VARIATION IN BOTH SIZE AND SHAPE OF *MICROTUS* LOWER M_1 THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT BOXGROVE.

Hypotheses 7.2 and 7.3 show that there is no statistical separation between stratigraphic levels at Boxgrove when the intraspecific shape or size of the M_1 is studied in isolation. In order to investigate further any further small-scale patterns within the dataset, samples are analysed in Procrustes form space, where log centroid size is included with the Procrustes-fitted landmark co-ordinates and the data are then analysed using PCA to provide an analysis of variance of both size and shape within a sample. Original centroid sizes can be seen in appendix C, and Eigenvalues for each PCA in table 7.15.

Figures 7.4 and 7.5 show principle components analyses in Procrustes form space for *M. agrestis* and *M. subterraneus* respectively. It can be seen that for both species there is a high degree of overlap of size and shape in form space between specimens from all stratigraphic levels. Cross-validation results (tables 7.16 and 7.17) show that specimens in form-space are unlikely to be assigned to the correct stratigraphic level (< 40 percent correct in all cases). Cross-validations performed in Procrustes form-space do not perform significantly better than those performed on Procrustes-fitted coordinates with size excluded (tables 7.13 and 7.14), suggesting that there is little co-variance between size and shape within this sample. The results of these analyses further support the suggestion shown in hypotheses 7.2 and 7.3 that the Boxgrove sample consists of an extremely uniform population with no observable inter-specific variability over time. Therefore hypothesis 7.4 cannot be rejected.

PC	Eigenvalues	% Variance	Cumulative %
1	0.00186642	34.44	34.44
2	0.00100569	18.56	53.00
3	0.00057009	10.52	63.52
4	0.00043022	7.94	71.46
5	0.00027631	5.10	76.56
6	0.00019111	3.52	80.08
7	0.00014927	2.75	82.83
8	0.00012307	2.27	85.10
9	0.00011413	2.10	87.20
10	0.00009674	1.78	88.98

PC	Eigenvalues	% Variance	Cumulative %
1	0.00101102	30.10	30.10
2	0.00062144	18.50	48.60
3	0.00036284	10.80	59.40
4	0.00020556	6.12	65.52
5	0.00018676	5.56	71.08
6	0.00013758	4.09	75.17
7	0.00010607	3.15	78.32
8	0.00009845	2.93	81.25
9	0.00009229	2.74	83.99
10	0.00008291	2.46	86.45

Table 7. 15 : Ten highest Eigenvalues for PC analysis in Procrustes form-space of Boxgrove M. agrestis (left) and M. subterraneus (Right) dataset including percentage of variation within the whole dataset explained by each PC and cumulative percentage.

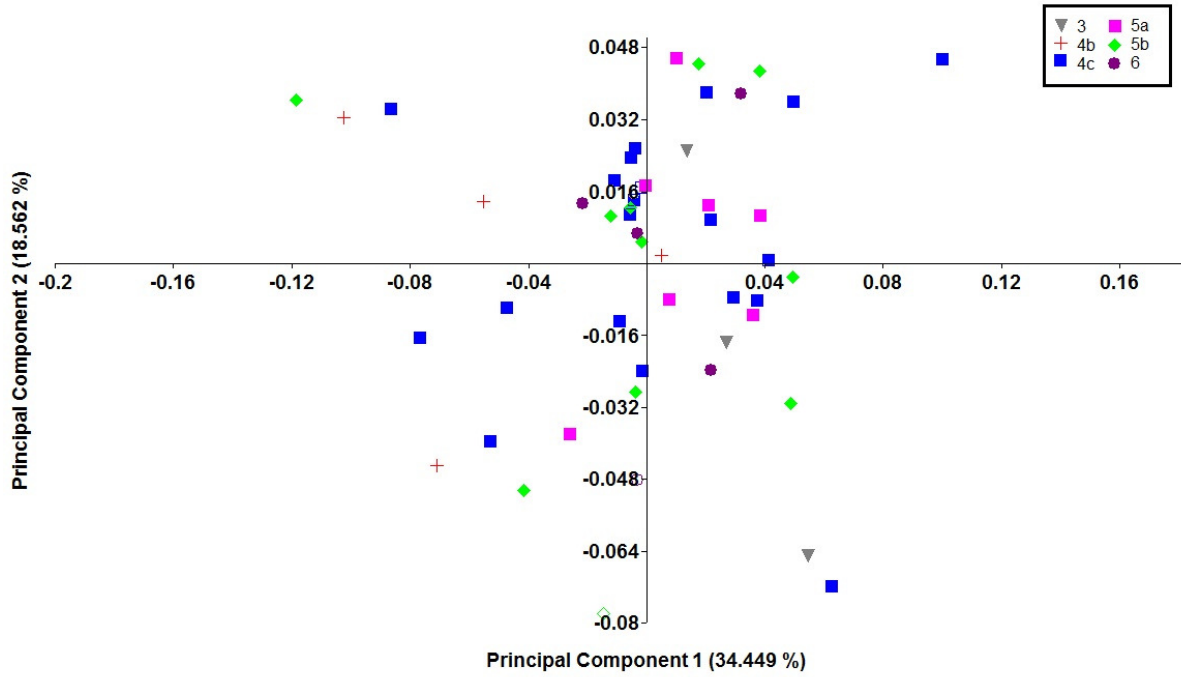

Figure 7.4: *Results of Principle Component analysis in Procrustes form space showing major axis of variation in the Boxgrove M agrestis dataset on PC1 and PC2 by stratigraphic level.*

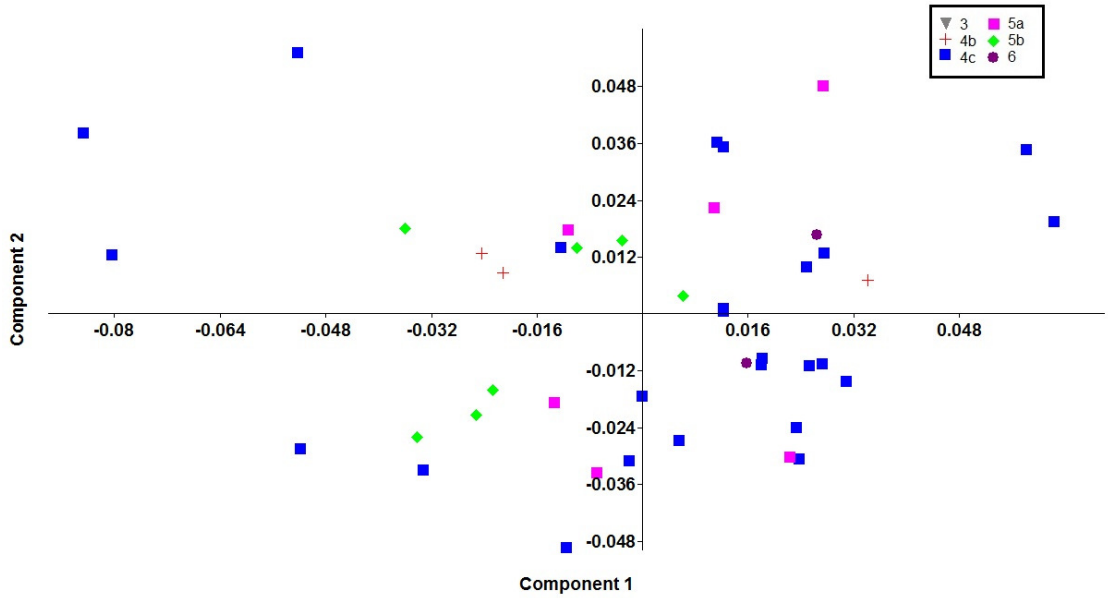

Figure 7.5: Results of Principle Component analysis in Procrustes form space showing major axis of variation in the Boxgrove M. subterraneus dataset on PC1 and PC2 by stratigraphic level.

	3	4b	4c	5a	5b	6
3	0.333	0.333	0.000	0.333	0.000	0.000
4b	0.400	0.400	0.000	0.200	0.000	0.000
4c	0.250	0.000	0.000	0.000	0.500	0.250
5a	0.000	0.000	0.286	0.000	0.429	0.286
5b	0.350	0.150	0.000	0.250	0.100	0.150
6	0.182	0.273	0.182	0.182	0.000	0.182

Table 7.16: *Results of a cross-validation analysis of Boxgrove M. agrestis in Procrustes form-space by stratigraphic level. Values are shown as proportion of samples from a sample assigned to each sample.*

	4b	4c	5a	5b	6
4b	0.333	0.000	0.333	0.333	0.000
4c	0.042	0.292	0.250	0.250	0.167
5a	0.167	0.333	0.000	0.500	0.000

5b	0.333	0.333	0.000	0.000	0.333
6	0.167	0.000	0.167	0.333	0.333

Table 7.17*: Results of a cross-validation analysis of Boxgrove M. subterraneus in Procrustes form-space by stratigraphic level. Values are shown as proportion of samples from a sample assigned to each sample.*

7.3.5. HYPOTHESIS 7.5: THERE IS NO SIGNIFICANT DIFFERENCE IN THE INTRASPECIFIC VARIATION OF SIZE IN *MICROTUS* LOWER M_1 TEETH AT BOXGROVE CAUSED BY CLIMATE.

In order to evaluate the statistical significance of change in size between temperate and cool stratigraphic levels, as determined by Taxonomic Index Scores (Roberts & Parfitt, 2009, see section 4.3 for further details), a Student's t-test is performed on the centroid sizes of *M. agrestis* and *M. subterraneus* datasets separately in order to evaluate the significance of any differences in the mean size of populations from cold and temperate conditions.

Within each dataset, specimens from all cool stratigraphic levels are combined, as are those from all temperate stratigraphic levels, to produce temperate and cool datasets for each species, as previous research has identified an overall increase in the size of Microtine rodents in warmer conditions and a decrease in cooler conditions (Mc Guire, 2009; Montuire *et al.*, 2004).

Table 7.19 shows the results of the Student's t-tests performed between the centroid sizes of the specimens from temperate and cool stratigraphic levels (original centroid sizes are shown in table 7.18). These results show no statistically significant difference in size between specimens from temperate or cool levels in either *M. agrestis* or *M. subterraneus*. Therefore, hypothesis 7.5 cannot be rejected on the basis of the results of this analysis.

Cold	Temperate
2310	1910
2390	2300
2320	2240
2630	2530
2470	2750
2400	2340
2330	1910
2550	2370
2300	2150
1760	2260
2390	2330
2280	2440
2400	2420
2440	2560
2370	2020
2340	2540
2700	2270
2260	2360
	2270
	2560
	2280
	2410
	2260
	2330
	2410
	2270
	2270
	2640
	2820
	2080
	2430
	2020

Cold	Temperate
2060	2020
2100	2340
2220	2300
2270	1960
2150	2060
2280	2000
2280	2010
2380	2420
2180	2410
	2320
	2130
	2550
	2040
	2040
	2650
	2220
	2230
	2110
	2080
	2110
	1930
	2060
	2130
	2090
	2160
	2030
	2150
	2080
	2040
	2120
	2120
	2210
	2180
	2210

Table 7.18: *Centroid sizes of M. agrestis (left) and M. subterraneus (right) specimens used in Student's t-tests to distinguish between temperate and cool levels.*

	t-value	Df	p-value
M. agrestis	0.540556539	48	0.591313
M. subterraneus	-0.89223956	41	0.377471

Table 7.19: *Student's t-test analysis of M. agrestis and M. subterraneus datasets, showing no statistical significance in size between specimens from temperate and cool environments.*

7.3.6 HYPOTHESIS 7.6- THERE IS NO SIGNIFICANT DIFFERENCE IN THE INTRASPECIFIC VARIATION OF SHAPE IN MICROTUS LOWER M_1 TEETH AT BOXGROVE CAUSED BY CLIMATE.

As shown in previous hypotheses, no clear separation of specimens from cool and temperate environments can be seen on PC1 and PC2, or any other principal components.

In order to evaluate if there is a statistically significant difference in shape between specimens from temperate and cool environments, as suggested by studies undertaken on other *Microtus* species (Montuire *et al.*, 2004; McGuire, 2009) a discriminant function analysis is performed (Table 7.20). This identifies no significant difference in shape between specimens from temperate and cool environments. Cross validation results (table 7.21, 7.22) show that samples are assigned to the correct group approximately 50% of the time, indicating that the strength of the discriminant function is poor.

In order to investigate any morphological changes within the Boxgrove *M. agrestis* and *M. subterraneus* datasets further, the amount of variance in M_1 shape in each climatic variable is investigated. Variance values are calculated from Procrustes-fitted landmark co-ordinates and then a bootstrap analysis is repeated one thousand times. The number of Bootstrap results for each variance figure are then plotted to produce a variance curve, as shown in figures 7.6 and 7.7 for *M. agrestis* and *M. subterraneus* respectively. The variance curves show that, in both *M. subterraneus* and *M. agrestis*, the amount of morphological variance in temperate and cold conditions is extremely similar. However, in *M. agrestis*, the variance in specimens from cold levels is reduced in comparison with specimens from warmer levels.

Therefore, on the basis of the results outlined above, it appears that temperature is not the main factor explaining shape variation in *Microtus* M_1 teeth within this data set, and H 7.6 cannot be rejected.

Species	Malahanobis' D2	Procrustes distance	p-value
M. agrestis	45.6277	0.01790725	0.2377
M. subterraneus	8.1543	0.02646362	0.9681

Table 7.20: *Results of a cross-validation analysis of Boxgrove M. agrestis and M. subterraneus by climate. Values are shown as proportion of samples from a sample assigned to each sample.*

	Warm	Cool
Warm	0.48	0.52
Cool	0.55	0.45

Table 7.21: *Results of a cross-validation analysis of Boxgrove M. agrestis by climate. Values are shown as proportion of samples from a sample assigned to each sample.*

	Warm	Cool
Warm	0.51	0.49
Cool	0.47	0.53

Table 7.22: *Results of a cross-validation analysis of Boxgrove M. subterraneus by climate. Values are shown as proportion of samples from a sample assigned to each sample.*

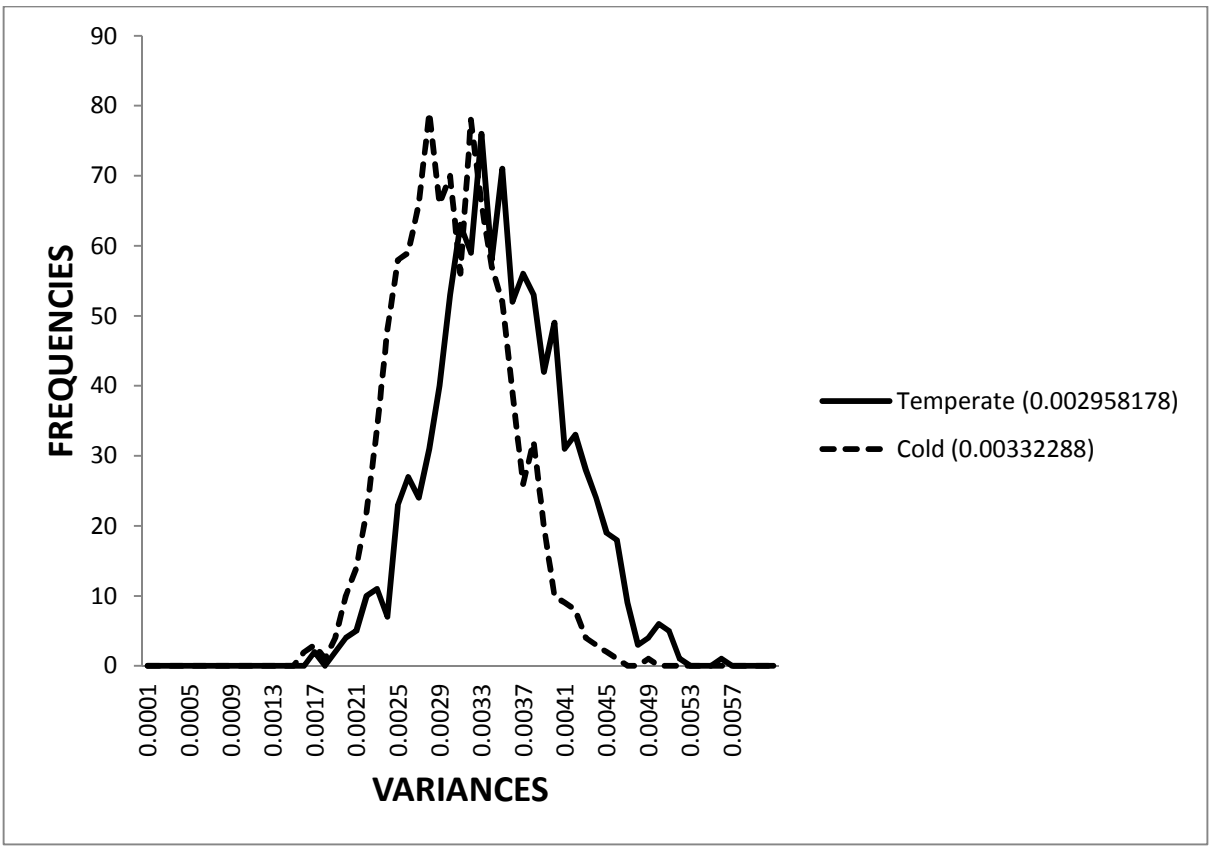

Figure *7.6: Variances in shape space for Boxgrove M. agrestis by climatic conditions and their bootstrap distributions. Bootstrap distributions for the shape variances of the 5 different groups(1000 bootstraps each; colour coding shown in key followed by original variance value).*

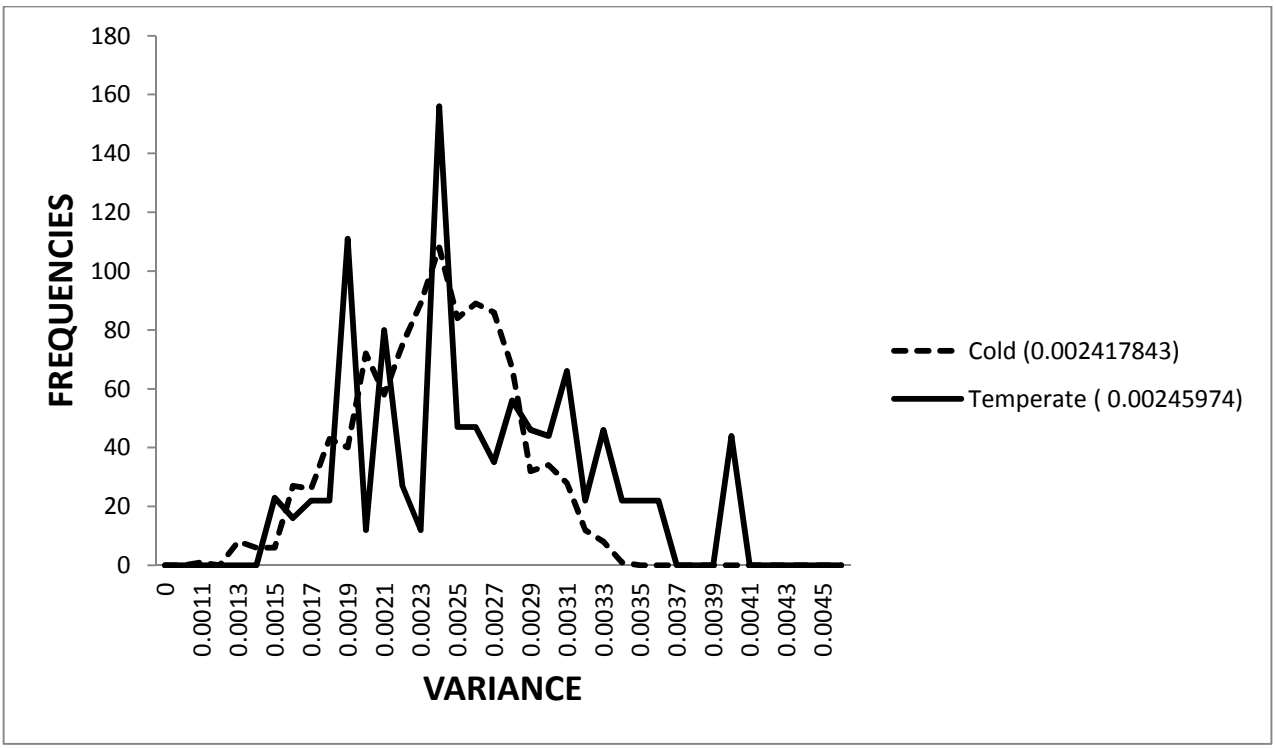

Figure 7.7: Variances in shape space for Boxgrove M. subterraneus by climatic conditions and their bootstrap distributions. Bootstrap distributions for the shape variances of the 5 different groups (1000 bootstraps each; colour coding shown in key followed by original variance value).

7.4 DISCUSSION

Throughout the Boxgrove dataset, in all analyses, very little variability in morphology or size of the M_1 has been identified using GMM analyses. The sample is extremely uniform throughout all stratigraphic levels. By comparison, both the modern and the Walou cave datasets examined earlier in this study display a large degree of intraspecific variation.

In analysing the factors that affect the archaeological assemblage at Boxgrove, it is extremely difficult to isolate those which may be driving the small amount of

morphological variability that has been identified. The very nature of archaeological material means that the time period represented by each stratigraphic level is unknown, and each may have been deposited very rapidly or represent an extended period of time. Equally, climatic reconstructions rely upon the validity of using modern-day ranges of species to reconstruct the ranges of populations in the past (Evans *et al.*, 1981). When morphological change is observed, it is not always possible to determine if that change is genetic, epigenetic or entirely environmental. However, some broad conclusions may be made, as will be discussed below.

Within the Boxgrove dataset, a very small allometric component is observed in samples from *M. agrestis*, *M. arvalis* and *M. gregalis* (< 5% for each sample). This is in agreement with the results found both from the Modern and Walou Cave samples (Chapter 3, H 3.2; Chapter 4, H 4.1), with the exception of *M. subterraneus*. The fact that the range of allometry found within a single site, at Boxgrove, is in line with that found within the entire modern datasets for most species is of interest, as it suggests that allometry is relatively static within most species. However, as discussed in chapter 3, modern *M. subterraneus* is far more allometric than any other species of *Microtus* (>13%), which is not reflected within the Boxgrove sample. The reason for the difference in the degree of influence of size upon shape between the samples is not clear simply from analyses of allometry, and may be down to genetic or environmental factors. However in other small rodents, such as mice, the majority of variability in tooth size is genetically determined (Bader and Lehmann, 1965). This marked difference between modern and Boxgrove *M. subterraneus* populations will be discussed further in Chapter 9, where the taxonomic relationships between modern and archaeological specimens are considered.

The size of *Microtus* M_1 teeth cannot be correlated with climatic conditions and does not appear to change significantly throughout the stratigraphic sequence at Boxgrove. Bergman's rule states that for mammals living in cooler conditions it is advantageous to become larger than their temperate-climate counterparts, because a larger body mass to surface area ratio will radiate less body heat per unit of mass (vice versa for individuals living in temperate climates; Bergman, 1874) . Tooth size in *Microtus* is known to increase with increased body-mass (Gromov and Polyakov, 1992), so it can be expected that individuals from stratigraphic levels that represent temperate phases would be smaller than their cooler-climate counterparts. In their study of *Microtus grafi* at the site of Bacho Kiro in Bulgaria, Nadachowski (1984) and Mointure & Brunet-Lecomte (2004) found that the opposite relationship is true and that individuals from temperate stratigraphic levels are slightly larger than those from cooler levels.

However, neither appears to be true of the individuals within the Boxgrove datasets, as the p-values gained from a student's t-test of centroid sizes shows that there is no statistically significant difference between the mean centroid sizes of individuals from temperate and cool climates, which is unsurprising, given the extremely small amount of variability in size throughout the whole Boxgrove sample. Figures 7.7 and 7.8 show a reduction of variance in cold environments compared with specimens from temperate environments in *M. agrestis*. This reduction in variance observed in cold conditions in in line with results found for *Microtus grafi* in Bulgaria where reduced morphological variance in cold conditions was observed. This reduction in cold conditions has several possible causes; firstly, although the species within this study can survive in a range of temperatures and climatic conditions, they are largely mesophillic. Under warmer climatic conditions, resources are likely to increase, leading to decreasing interspecific

competition for resources. This could allow either a new morphology to be expressed *in situ* or could lead to increased population sizes and therefore, increased genetic mixing between populations (Nadachowski, 1984; Spears & Clarke, 1987; Mointure & Brunet-Lecomte, 2004). Therefore, it is suggested that although climate is not likely to have a direct effect upon M_1 morphology, its effects on factors such predation, competition, maturation rate and mixing between populations may indirectly influence the amount of shape variance seen in the M_1.

There are several possible explanations for the uniformity of M_1 size across temperate and cool environments. Gene flow from other populations may have occurred throughout the stratigraphic sequence and genetics may have been the dominant factor affecting the size of the individuals, rather than climate. It is also possible that the variation in size between temperate and cool levels is too small to measure accurately using the centroid size, particularly on the relatively small sample sizes (<50 individuals of each species in total), if one is present at all. However, on the basis of the evidence from Boxgrove, the most likely explanation is that there is no influence of climate upon the size of the M_1 within the *Microtus* species included within this study. As body-mass change within *Microtus* species relating to climatic conditions is well studied in *Microtus* populations, it is also possible that body size or mass may have been affected by climatic conditions but that this change in size is not mirrored by a corresponding change in the size of the M_1, and therefore is not identified within this study.

When analysing the change in shape of *Microtus* teeth throughout the stratigraphic sequence, the PCA of the *M. agrestis* and *M. subterraneus* datasets each show no clear separation between stratigraphic levels on any single or combination of principal

components. Discriminant function analysis shows no statistically significant Malahanobis' distances between stratigraphic levels as based on M_1 morphology. PCs 1 and 2 from the PCA account for 32% and 43% of the overall variation within the *M. agrestis* and *M. subterraneus* datasets respectively. Analyses performed in Procrustes form-space, where both size and shape of the specimens are taken into account, also show no clear distinction between stratigraphic levels and, conversely, in climatic conditions.

Similarly, when the datasets are grouped by climate, there are also no distinct groups seen on Principal Components 1 and 2 or any alternative combination of PCs, and discriminant function analyses also show no statistically significant difference between the two climate groupings. Analyses of variance show that the amounts of variance seen in warm and cold environments and, also, between stratigraphic levels are extremely similar, when the effects of small sample size are taken into account. Throughout all analyses, cross-validation results show that the ability to assign specimens to the correct climatic or stratigraphic group is very poor.

These results may correlate with the findings of Polly *et al.* (2011) that the majority of the variance of morphology in *Microtus* molars (70-80%) is heritable, depending on species, and that the remaining 20-30% of M_1 shape is ecophenotypic in nature. There is clearly some factor controlling the majority of the variation in shape which is not explained by climate or the age of the specimens. It is not possible, with the present data, to say whether this factor is genetic or environmental. As it has been shown in chapter 5 that there is a very large amount of inter and intra-specific variation in Modern populations of *Microtus*, it is likely that the lack of distinction between samples at Boxgrove is likely to be a factor of both the small available sample size and

also the relatively short time-span represented by the samples. Overall, the *Microtus* remains from Boxgrove have been shown to be a very homogeneous sample with a little or no variation throughout the sequence.

In all the analyses described above, and their associated interpretations, it should be noted that *Microtus* remains have only been recovered in relatively small sample numbers for many of the stratigraphic levels at Boxgrove means that results which are statistically insignificant may be a consequence of low sample numbers. The possibility that larger sample sizes may have produced significant results cannot be ruled out in this case study. Therefore, the next chapter will attempt to answer similar questions, using a much larger dataset from a site of a similar age to Boxgrove, at Westbury Sub-Mendip.

7.6 CONCLUSIONS

- The Boxgrove sample is an extremely homogenous sample with no statistically significant change in either the shape or size of *Microtus* M_1 teeth related to stratigraphic level or climatic conditions.

CHAPTER 8
CASE STUDY 3- WESTBURY SUB-MENDIP

8.1 INTRODUCTION

Chapters 4-7 have identified the patterns of morphological variation associated with both environmental and evolutionary change within both modern and archaeological material, and attempted to identify the same patterns of variation in Archaeological material. Within the archaeological datasets from Walou Cave and Boxgrove, very few patterns to the variance have been identified, possibly as a result of small sample sizes. This chapter aims to investigate the same questions posed of previous datasets and ask them of the much larger sample from Westbury sub-Mendip.

Westbury is a large cave site, containing a complex sequence of stratigraphic levels covering over 30 metres laterally and 70 metres horizontally. The site was discovered during quarrying activities, which exposed the profile of the stratigraphic sequence of sediments filling the cave. The stratigraphic sequence at Westbury was extremely complex and interpretation is further complicated by the presence of 3 different excavation sites, for which correlations between stratigraphic units are not always clear. Therefore, analyses within this chapter, seek to differentiate between stratigraphic levels and samples from different climatic conditions.

The sequence at Westbury covered several different climatic episodes ranging from temperate to cold (as discussed in section 8.2). The climatic conditions for each level are reconstructed on the basis of sedimentology and the habitats and tolerances of the

vertebrate taxa present, with the assumption that modern preferences reflect those of the past species, known as the Taxonomic habitat Index.

Previous analyses on the sites at Boxgrove and Walou cave (chapters 7 and 6) show very little differentiation in the morphology of *Microtus* M_1 remains from different stratigraphic levels at the site, or correlating with climatic conditions. This is in contradiction with the data suggested by previous studies (Renaud, 1999; McGuire, 2009), where climatic conditions have been shown to influence M_1 morphology, and in what we would expect from a genus which is known to evolve extremely rapidly and to have high inter and intra-population variability in M_1 shape (Chaline and Graf, 1988; Chaline et al., 1999)**.**

However, it is possible that at least some of the perceived homogeneity of the samples at Boxgrove and Walou Cave is due to the relatively short time period represented by the remains and small sample sizes respectively. The *Microtus* remains from Westbury, being both extremely abundant and also covering a large time period with several clearly defined climatic fluctuations, represent an opportunity to resolve some of these issues. Therefore, as with previous datasets, this chapter aims to investigate the standard sequence of questions and accompanying hypotheses**:**

1) Evaluation of the effect of size upon M_1 shape in *Microtus* species.

As discussed within previous chapters, it is important to assess the degree of allometry present within the M_1 of the *Microtus* species included within this study, as, if a large allometric component is found within the data, it may be desirable to remove the

allometric component to the data in subsequent analyses (e.g. Penin et al. 2002; Frost et al. 2003; Mitteroecker et al. 2004).

The Walou, Modern and Boxgrove datasets (analysed in chapters 4 and 5 of this study) have demonstrated c. 5% of the shape variance observed within PC1 being explained by size . At Westbury, we may expect to see a similar amount of allometry present, if <5% of morphological variance is standard in the *Microtus* species within this study, and therefore is not affected by genetic, climatic or geographic factors.

Hypothesis 8.1- *There is no significant allometric component to intraspecific diversity in Microtus lower M_1 morphology at Westbury.*

If an allometric component is found within the Boxgrove datasets, further analyses will be performed in order to investigate the reasons for variance in both size and shape at Westbury.

2) Evaluation of the effect of external environmental factors, such as prevailing climate upon the morphology of the *Microtus* M_1.

Distinct morphological changes in the morphology of *Microtus* dentition attributed to climatic change have been demonstrated in more than one study (Mc Guire, 2009; Montuire et al., 2004). *Microtus* species have also been shown to increase in size in warmer conditions and decrease in cooler ones, the opposite of what might be predicted by Bergman's Rule (Bergman, 1847). Therefore, an alternative explanation for morphological change in shape or size of *Microtus* teeth throughout the stratigraphic sequence at Westbury is that climatic factors have an influence upon

epigenetic variation. Several studies have shown that *Microtus* teeth display a relatively low degree of epigenetic variation (Uhlikova, 2004). Therefore, it is possible that the size of *Microtus* teeth may also change in line with general body-size change in response to the prevailing climatic conditions.

Therefore, it may be possible to identify specific morphological changes or changes in size which are associated with climatic conditions in *Microtus* species.

The Westbury sequence contains more than one climatic episode, with an intervening cool period (Andrews & Stringer, 1999). Therefore, on the basis of the literature and discussion cited above, we would expect there to be some morphological change related to climatic conditions within the Westbury populations.

Hypothesis 8.2: *There is no significant intra-specific variation in Microtus lower M_1 tooth size caused by climate at Westbury.*

The size of *Microtus* M_1 teeth throughout the stratigraphic sequence at Boxgrove will be analysed for each species separately, using climatic reconstruction as analysed by Andrews, 1999 based upon the taxonomic habitat index (Evans, 1981; Andrews, 1990).

Hypothesis 8.3: *There is no significant intra-specific variation in Microtus lower M_1 tooth morphology caused by climate at Westbury.*

If hypotheses 8.2 and 8.3 show no clear indication of morphological evolution or change in size according to climate, the co-variance of both size and shape will be examined, in Procrustes Form Space;

Hypothesis 8.4: *There is no significant co-dependent, intraspecific variation in both size and shape according to climate at Westbury.*

3) To evaluate the current stratigraphic model of the Westbury sediments and the degree of morphological change present throughout the stratigraphic sequence at Boxgrove.

As is common in most cave sites, the stratigraphic sequence at Westbury is extremely complex, with many units and sub-units being identified within the stratigraphic sequence. Due to the nature of the site and extensive damage due to quarrying activity, excavations were undertaken in several different localities (See chapter 2 for stratigraphic descriptions). As correlations between the sequences could not always be observed laterally and were not always clear, correlations between stratigraphic levels at different sites were made on the basis of soil colour, composition and faunal remains (Andrews et al, .1999). Andrews (1990) determined a stratigraphic summary of the site from these laterally discontinuous excavations, based upon lithological, sedimentological and mammalian evidence.

Geometric morphometric analysis of specimens from different excavation locations that are thought to be from the same stratigraphic level may provide evidence to support or refute the current stratigraphic reconstruction at the site.

If specimens from different excavation locations that are believed to represent the same stratigraphic level show no significant difference in morphology, then the following areas will be investigated.

As discussed in detail within chapter 1, the use of the dental evolution of Microtine rodents as a relative dating tool is well studied (e.g. ; Fejfar & Heinrich, 1983; Heinrich,1990; von Koenigswald & van Kolfschoten , 1996;). However, this is an area

that has not been studied in any detail in *Microtus* species. As we know *Microtus* species are known to evolve extremely rapidly, and this evolution is reflected within their dental morphology (Chaline et al., 1999), there is potential for evolutionary morphological change to be identified within *Microtus* across a long time sequence at a single site, such as Westbury. The *Microtus* remains from Westbury have particular potential for identifying any morphological changes which could be utilised in relative-dating due to the extremely abundant *Microtus* remains recovered at the site throughout the majority of the stratigraphic sequence. The patterns of morphological differentiation between stratigraphic levels at Westbury may also provide a method of solidifying the complex stratigraphy at the site, and in providing correlation between levels from different excavation sites, for which the relationship may not always be clear.

Hypothesis 8.5*: There is no significant intraspecific variation in size of the M_1 throughout the stratigraphic sequence at Westbury.*

Hypothesis 8.6- *There is no significant intraspecific variation in shape of the lower M_1 throughout the stratigraphic sequence at Westbury.*

In order to investigate further any morphological differences between *Microtus* populations throughout the stratigraphic sequence at Westbury, the following hypothesis will be erected;

Hypothesis 8.7: *There is no significant intraspecific, co-dependent variation in both size and shape of Microtus lower M_1 throughout the stratigraphic sequence at Westbury.*

8.2 MATERIALS AND METHODS

A brief description of sample composition and methods of analysis are provided below.

8.2.1 MATERIAL

A sample of 688 *Microtus* specimens is selected from throughout the stratigraphic sequence at Westbury. Sample sizes for each stratigraphic level can be seen in table 8.1.

	10	11	12	13	14	15-1	15-2	15-3	15-4	15-5	15-8	18	19/13	19/14	19/15	20	TOTAL
M. arvalis/ agrestis	9	35	24	15	16	14	30	*	20	8	20	*	8	18	*	*	217
P. gregalodies	40	26	36	37	45	7	2	13	6	*	24	28	4	40	12	32	352
M. subterraneus	6	*	8	6	8	16	37	*	26	12	*	*	*	*	*	*	119

Table 8.1: *Summary of sample sizes for each species of Microtus throughout the Westbury Stratigraphic sequence.*

The sample of small mammal remains recovered from Westbury during excavation is extremely large. The large number of microfaunal remains at the site can be attributed to birds of prey and small carnivores roosting/ denning within the cave system and depositing small mammal remains in their faeces (Andrews, 1990). Microfaunal remains were recovered from the site by sieving of bulk sediment samples once removed from the site. Breakage and damage to the remains from the site is common, possibly due to the sieving techniques used, however, the extremely large sample sizes available mean that it is possible to recover large samples of undamaged specimens for all species from most stratigraphic levels. The sample sizes for each species within this study are a proportional representation of the overall Westbury assemblage.

P. gregaloides is relatively uncommon within the British Pleistocene, however is extremely common within the Westbury sediments. *M. arvalis/ agrestis* are also found in relatively large numbers throughout the sequence, with *M. subterraneus* being comparatively rarer.

The climatic conditions assigned to each stratigraphic level used within this study are shown in table 8.2. Levels designated as Temperate contain species which are indicative of climatic conditions as warm, or warmer than the present day within the UK, whereas Cool/ Temperate levels contain species which indicate cooler conditions than found within present day UK without being as cool as the Cold levels which contain a high percentage of tundra and steppic faunal remains (Andrews and Stringer, 1999).

Unit	Climate
20	Temperate
19	Cool-Temperate
18	Cold
15/8	Cold
15/4	Temperate
15/3	Cool-Temperate
15/2	Temperate
15/1	Cool-Temperate
14	Cold
13	Cool-Temperate
12	Temperate
11	Temperate
10	Cool-Temperate

Table 8.2: *Summary of Climatic conditions for each stratigraphic level analysed within this study at Westbury cave (Adapted from Andrews and Stringer, 1999, p. 207).*

8.2.2 METHODS

As found in the other sites examined, the Westbury sample contains material assigned to *M. arvalis/ agrestis* on the basis of M_1 morphology as the two species are not easily differentiated from isolated teeth, without corroborative evidence from M^2 morphology. Using the methodology outlined in section 4.7, a discriminant function is run on modern *M. arvalis*, *M. agrestis, M. gregalis* and *M. subterraneus* samples. The combined *M. arvalis/ agrestis* dataset from Westbury is then split into species using the discriminant function. All specimens from Westbury are assigned to *M. agrestis*, with *no M. arvalis* specimens being identified. As the discriminant function is extremely robust in modern material ($p = <0.0001$) and has been shown to be consistent under varying conditions in archaeological material (see chapters 6 and 7), and given that there are *no M. arvalis* M^2 teeth reported in the literature (Andrews, 1990; Currant, 1999) for this site, it can be assumed that the sample consists of a single species. Further discussion of the taxonomic implications of this result can be found in Chapter 9. A summary of the species and specimen numbers at Westbury used in these analyses can be seen in Table 8.3.

All specimens are recorded using photographs and 15 homologous landmarks placed on each specimen, with a further 10 semi-landmarks placed around the AC region of the tooth to fully capture the shape variation within the samples (Figure 3.2). All analyses of shape are conducted using the full set of landmarks

In all analyses, specimens are firstly superimposed using Generalised Procrustes Analysis (GPA) to remove the effects of size, translation and orientation upon the

dataset prior to further analysis. During GPA, the centroid size of each specimen is retained for use in further analyses, as discussed below.

The analyses in this chapter utilise the full Westbury dataset of 688 specimens. Summary data of the sample composition can be seen in Table 8.3. Twenty-five landmarks are collected from each tooth, as described in chapter 3, comprising 15 fixed landmarks and 10 semi-sliding landmarks along the curve of the AC region.

In all analyses, landmarks are firstly superimposed using Generalised Procrustes Analysis (GPA) to remove variation due to translation and rotation and to separate shape from size.

In all samples, specimens recorded as *M. arvalis*/ *M. agrestis* due to the isolated nature of the M_1 teeth (and lack of associated M^2) are assigned to the correct species using the discriminant function methodology used in previous chapters. Discriminant functions generated from modern *M. agrestis*, *M. arvalis*, *M. gregalis* and *M. subterraneus* as discussed in chapter 4 (discriminant functions separating known species in the modern dataset $p < 0.0001$). The combined *M. arvalis*/ *agrestis* Westbury sample is then assigned to species using the modern discriminant function with each specimen treated as an unknown. The results of these analyses can be seen in appendix B.

Analysis methods within this chapter are outlined below;

H 8.1: In order to assess the allometric component within the species datasets, a multivariate regression of shape co-ordinates on centroid size is performed, using centroid sizes and shape coordinates. Centroid sizes are calculated during Procrustes'

fitting and are used as a measure of size, as they are a biologically meaningful expression of the overall scale of the landmark configuration. Shape change is visualised as Cartesian Transformation Grids calculated using thin plate splines.

H 8.2 & H 8.5: To calculate if there is a statistically significant difference in size, a Students' t-test is performed upon the centroid sizes of each sample, as calculated during the Procrustes fit of the combined samples.

H 8.3 & H 8.6: Principal Components Analysis (PCA) is performed using the Procrustes-fitted coordinates from the GPA to visualise the major axes of variation in the dataset. In order to investigate the variation within the datasets further, a discriminant function is performed using the Mahalanobis D2 distances between group means. To assess the power of the discriminant function, a discriminant function with leave-one-out cross-validation is carried out. To visualise the relative distances between groups, the unweighted pairgroup method using arithmetical averages (UPGMA) is used to produce phenographic trees showing relationships between species, explained in chapter 3. The UPGMA trees are calculated using the Procrustes distances between species datasets. All UPGMA trees are calculated using the landmark methodology on the basis of the full set of landmarks, as shown in chapter 3. A range of variance values is then calculated via bootstrapping the original data 1000 times. The bootstrap value are then plotted to provide curves illustrating the distribution of variance in shape-space for each sample.

H 8.4 & H 8.7: In samples where there appeared to be a difference in both shape and size, samples are analysed in Procrustes' Form-space. Log centroid size is included within a Principle Component Analysis of Procrustes-fitted coordinates. In order to

investigate the variation within the datasets further, a discriminant function is performed using the Mahalanobis D2 distances between group means. To assess the power of the discriminant function, a discriminant function with leave-one-out cross-validation is carried out.

	10	11	12	13	14	15/1	15/2	15/3	15/4	15/5	15/8	18	19/13	19/14	19/15	20	TOTAL
M. agrestis	9	35	24	15	16	14	30	•	20	8	20	•	8	18	•	•	217
P. gregalodies	40	26	36	37	45	7	2	13	6	•	24	28	4	40	12	32	352
M. subterraneus	6	•	8	6	8	16	37	•	26	12	•	•	•	•	•	•	119

Table 8.3: Summary of specimen numbers by stratigraphic level after separation of M. arvalis/ agrestis by discriminant function analysis.

8.3 RESULTS

8.3.1: HYPOTHESIS 8.1- *THERE IS NO SIGNIFICANT ALLOMETRIC COMPONENT TO INTRASPECIFIC DIVERSITY IN MICROTUS LOWER M_1 MORPHOLOGY AT WESTBURY.*

In order to assess the degree of allometry present within each species at Westbury, a multivariate regression of Procrustes coordinates onto centroid size is performed. As shown in table 8.4, the percentage of shape variance within each sample that is explained by size is relatively low in all species, at < 3%. In *P. gregalodies and M. subterraneus* samples, the amount of allometry within the samples is so low (0.4222 and 1.2404% respectively) that it is shown to be statistically insignificant. However, within the *M. agrestis* sample, 2.5647% of the shape within the sample is shown to be statistically significant at 95% confidence.

This difference in the percentage of allometry observed between the different species samples does not appear to be linked to the range of centroid sizes observed within each species (Table 8.5) or the number of specimens present within each sample. The percentage of shape explained by size within the Westbury species samples is within the ranges observed within the Walou cave (6.3.1) and Boxgrove (7.3.1) samples and smaller than that found in modern samples.

To visualise the shape change between the smallest and largest specimens in each sample, the specimen with the largest and smallest centroid size within each species is plotted as a change from the mean shape of the sample. Figures 8.1-8.3 show shape variation from smallest to largest specimens in each species as Cartesian transformation grids, calculates as thin plate splines. All three species display similar changes in shape in larger specimens compared to smaller ones. In the larger specimens, there is very little relative morphological difference in triangles 1-5,

whereas the anteroconid complex (AC) becomes proportionally smaller and relatively tilted towards the buccal surface of the tooth. Re-entrant angles 4 and 5 also become less pronounced in the larger specimens compared to the smaller specimens.

On the basis of the evidence presented above, the amount of allometry within the samples (although shown to be statistically significant in *M. agrestis*) is not considered to be large enough to require removal of the allometric effect within subsequent analyses, as PC1 accounts for a relatively large proportion of variance observed within each dataset (16, 30 and 16 % for *M. agrestis*, *P. gregalodies* and *M. subterraneus* respectively), whereas only a small proportion of the total variation in the dataset can be explained by allometry. Therefore, on the basis of the evidence presented above, Hypothesis H8.1 is rejected.

Species	Total % predicted	p-value
M. agrestis	2.5674	<0.0001
M. subterraneus	1.2404	0.1288
P. gregalodies	0.4222	0.2121

Table 8.4: *Results of Multivariate regression of Procrustes co-ordinates onto centroid size for all Westbury species. Statistically significant p-values are highlighted in yellow.*

Species	Max. Size	Min. Size	Range
M. agrestis	0.0849	0.818	0.022
M. subterraneus	0.842	0.81	0.032
P. gregalodies	0.084	0.818	0.022

Table 8.5: *Minimum, maximum and range of centroid sizes for each Microtus species at Westbury*

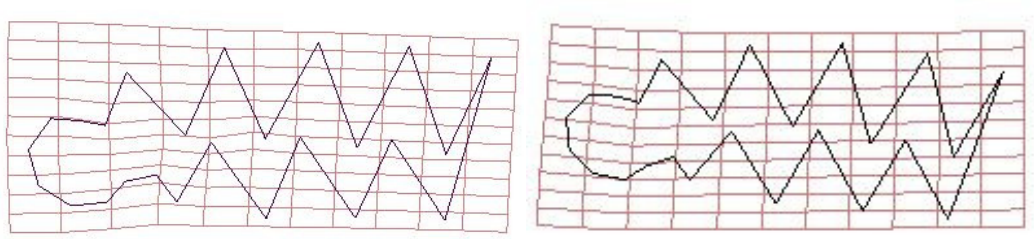

Figure 8.1: *Cartesian transformation grids illustrating variation in shape from mean shape between the smallest (left) and largest (right) M. agrestis specimens from Westbury sub-Mendip.*

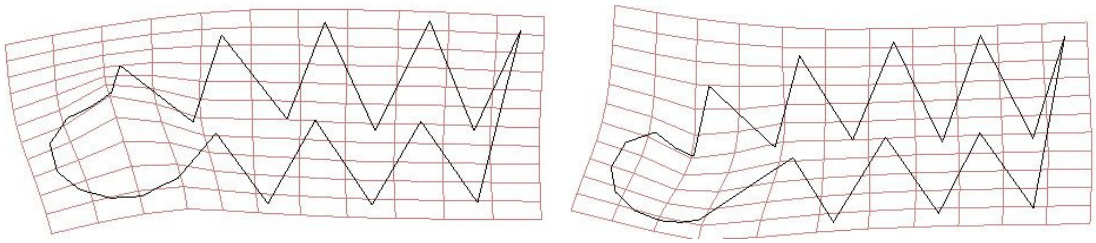

Figure 8.2: *Cartesian Transformation Grids illustrating variation in shape from mean shape between the smallest (left) and largest (right) P. gregalodies specimens from*

Westbury sub-Mendip.

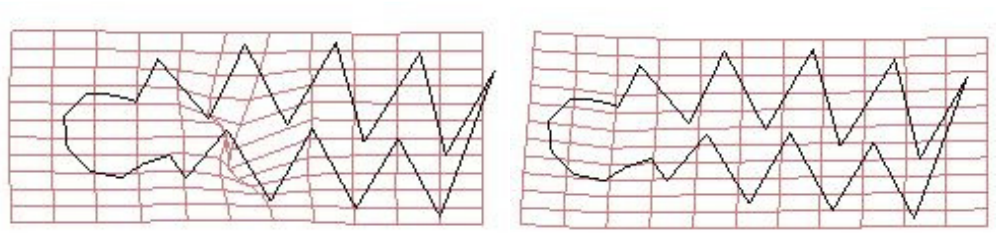

Figure 8.3: *Cartesian Transformation Grids illustrating variation in shape from mean shape between the smallest (left) and largest (right) M. subterraneus specimens from Westbury sub-Mendip.*

8.3.2 HYPOTHESIS 8.2: *THERE IS NO SIGNIFICANT INTRA-SPECIFIC VARIATION IN MICROTUS LOWER M_1 TOOTH SIZE CAUSED BY CLIMATE AT WESTBURY.*

In order to assess the effect of climatic conditions upon the size of *Microtus* M_1 teeth, a Students' t-test is performed upon the intraspecific centroid sizes of specimens from different climatic conditions, as reconstructed by Andrews et al.,(1999) using taxonomic habitat reconstruction.

The results of the Student´s T-tests for each species are shown in tables 8.6-8.8. Specimens from temperate and cold stratigraphic levels are statistically significantly different in size in all species ($p < 0.05$). In all species, there is no significant difference in size between Cold and Cool/ Temperate levels. The mean values for each climatic sample show there is a clear difference in the mean size of the specimens from warm and cold stratigraphic levels in all species (Table 8.9). Within all species, the largest range of sizes is found within temperate conditions, with variability in size becoming reduced in cooler conditions.

In *P. gregalodies*, there is also a statistically significant difference between specimens from Temperate and Cool/ Temperate levels, and a corresponding large difference in the mean shape of the samples is found (table 8.9). As both samples are relatively large, it is unlikely that this result is an artefact of sample size, particularly as the range of sizes within the samples is similar. It should also be noted that the difference between cold and temperate levels within *P. gregalodies* is much smaller than that found in the *M. agrestis* and *M. subterraneus*. As all sample sizes are large and relatively equal (circa 100 specimens), this smaller difference is likely to reflect a

reduced amount of size variance caused by climatic conditions in *P. gregalodies* rather than the reduced significance being a mathematical artefact of sample size.

Contrary to the assertion made by previous authors when studying other *Microtus* species (Montuire et al., 2004; McGuire, 2009), within all species included within this study, the largest specimens are found in cold conditions and the smallest in temperate conditions, as would be predicted by Bergmann's Rule (Bergmann, 1847) .

On the basis of the results presented above, hypothesis 8.2 is rejected and it is proposed that climatic conditions do affect the size of *Microtus* M_1 teeth, which become larger in cooler conditions and smaller in warmer conditions.

	Cold	**Temperate**
Temperate	*3.825*	
	0.000191476	
Cool/Temperate	*1.973*	*-1.675*
	0.063090679	**0.0957538**

Table 8.6: *p-values from a Students' t-test on the M. agrestis dataset from Westbury sub-Mendip. P-values are in bold and t-values in italics. Samples with significantly different centroid sizes (p<0.05) are highlighted in yellow.*

	Cold	**Temperate**
Temperate	*0.435*	
	0.0463768	
Cool/Temperate	*0.757*	*0.322*
	0.4494247	**0.747265563**

Table 8.7: *p-values from a Students' t-test on the P. gregalodies dataset from Westbury sub-Mendip. P-values are in bold and t-values in italics. Samples with significantly different centroid sizes (p<0.05) are highlighted in yellow.*

	Cold	Temperate
Temperate	*3.12*	
	0.002520254	
Cool/Temperate	*-0.37*	*-4.167*
	0.712139633	**0.0000684994**

Table 8.8: *p-values from a Students' t-test on the M. subterraneus dataset from Westbury P-values are in bold and t-values in italics. Samples with significantly different centroid sizes (p<0.05) are highlighted in yellow.*

	M. agrestis			*M. subterraneus*			*P. gregalodies*		
	sample size	Mean	Range	sample size	Mean	Range	sample size	Mean	Range
Temperate	109	0.827	0.032	60	0.819	0.028	100	0.828	0.023
Cold	43	0.83	0.019	20	0.824	0.02	105	0.83	0.02
Cool/Temperate	63	0.828	0.028	35	0.824	0.027	97	0.828	0.022

Table 8.9 Mean size and range of centroid sizes for each species at Westbury by climate.

8.3.3 HYPOTHESIS 8.3: *THERE IS NO SIGNIFICANT INTRA-SPECIFIC VARIATION IN MICROTUS LOWER M_1 TOOTH MORPHOLOGY CAUSED BY CLIMATE AT WESTBURY.*

In order to evaluate the differences in shape between specimens from different climatic conditions, PCAs are run for each species individually. In all species, no single PC is found to separate specimens from sediments representing distinct climatic conditions, necessitating further testing using discriminant functions. Eigenvalues for PCA can be seen in table 8.16.

Tables 8.10, 8.12 and 8.14 show the results of Discriminant Function analyses, assessing the significance of morphological differences between specimens of the same species in different climatic conditions. For all species, there is a statistically significant difference between specimens from cold and temperate conditions and also between temperate and cool-temperate specimens. In all instances, the separation between cold and temperate conditions is more statistically valid than between

temperate and cool-temperate conditions, which suggests that the greater the temperature difference between specimens, the greater the difference in morphology.

Tables 8.11, 8.13 and 8.15 show Cross validation results for *M. agrestis*, *P. gregalodies* and *M. subterraneus*. All results show that although the separation between the climatic conditions, as assessed by discriminant function analysis are considered to be statistically valid for all species, specimens are only correctly identified to their climatic group less than 50 % of the time.

Bootstrapped variance results (figures 8.4-8.6) show that the frequency of variances observed between the samples from differing climatic conditions is similar across all species. However, the original variances show that that in all species, the samples from cold conditions have a reduced variance compared to those from warmer conditions. This finding correlates with results found in Walou and Boxgrove samples.

Therefore, on the basis of the results outlined above, hypothesis 8.3 is rejected.

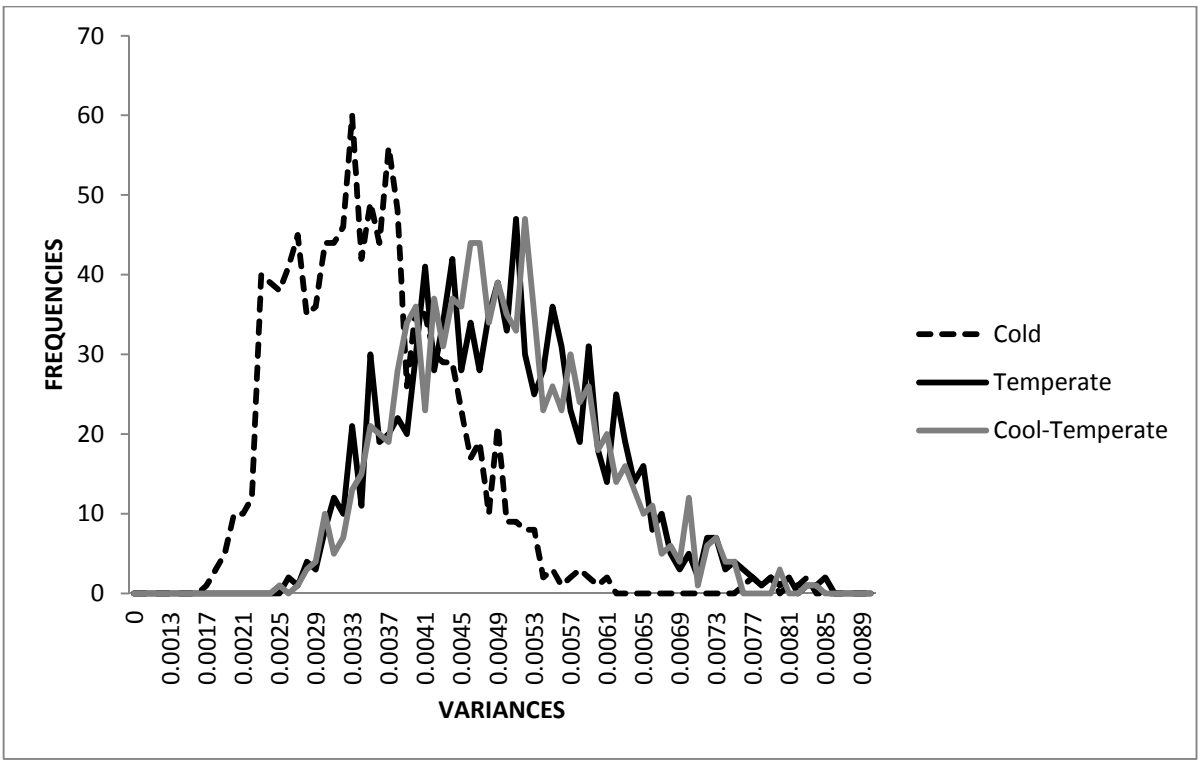

Figure 8.4: Bootstrapped variance frequencies for M. agrestis by climate at Westbury. Original variance values alongside corresponding value in the key.

	Cold	Cool-Temperate
Cool/Temperate	*0.01494455*	
	0.5719	
Temperate	*0.02056939*	*0.01209936*
	0.0001	**0.0338**

Table 8.10: *Discriminant function analysis results for M. agrestis at Westbury by climate. Procrustes distances (bold) and associated p-values (italics). Statistically significant results (p=<0.05) are highlighted in yellow.*

	Cold	Cool-temperate	Temperate
Cold	0.4186	0.2791	0.3023
Cool-temperate	0.2951	0.4098	0.2951
Temperate	0.4545	0.3273	0.2182

Table 8.11: *Results of a cross-validation analysis of M. agrestis from Westbury by climatic conditions. Values are shown as proportion of samples from a sample assigned to each sample.*

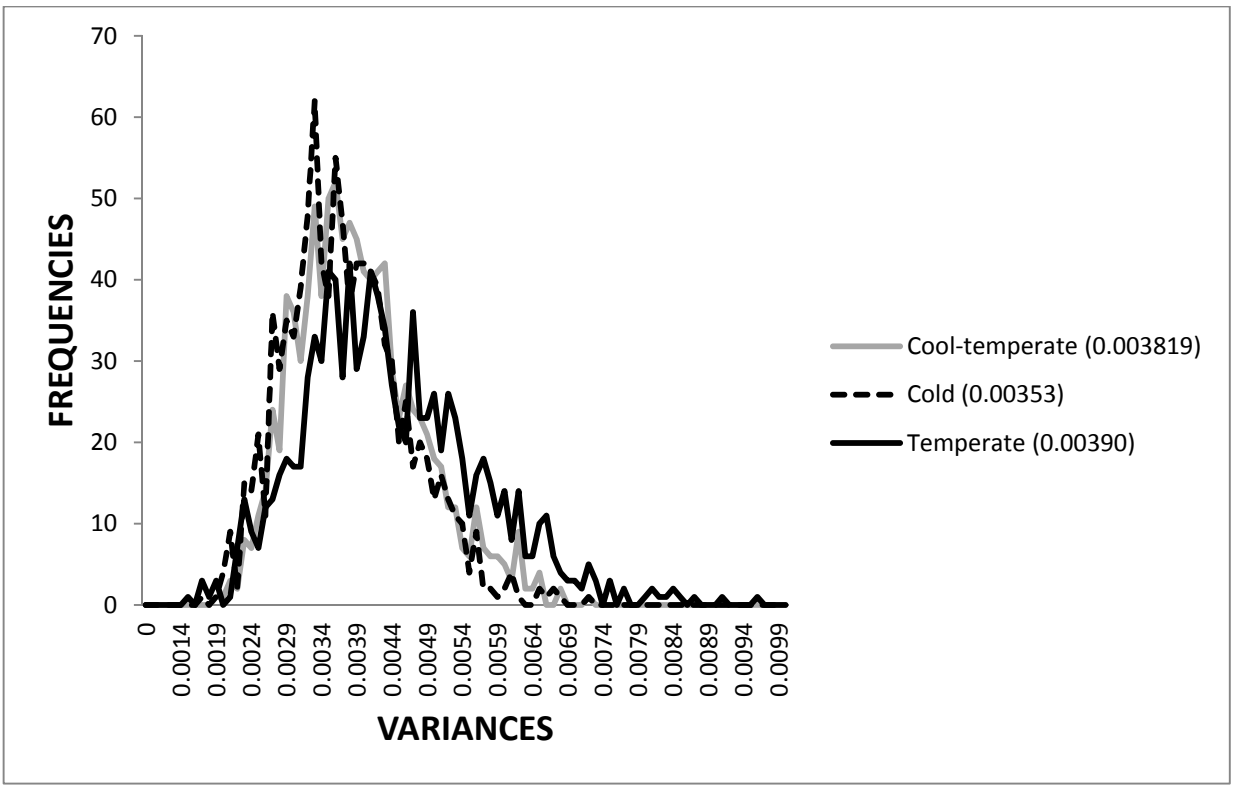

Figure 8.5: *Bootstrapped variance frequencies for P. gregalodies by climate at Westbury. Original variance values alongside corresponding value in the key.*

	Cold	Cool-Temperate
Cool/Temperate	**0.01086905**	
	0.1349	
Temperate	**0.01516838**	**0.01811354**
	<.0001	*<.0001*

Table 8.12: *Results of Discriminant Function analysis of P. gregalodies at Westbury by climatic conditions. Procrustes distances are shown in bold and associated p-values in italics.*

	Cold	Cool-temperate	Temperate
Cold	0.3714	0.3048	0.3238
Cool-temperate	0.3196	0.3711	0.3093
Temperate	0.3100	0.2900	0.4000

Table 8.13: *Results of a cross-validation analysis of P. gregalodies from Westbury. Values are shown as proportion of samples from a sample assigned to each sample.*

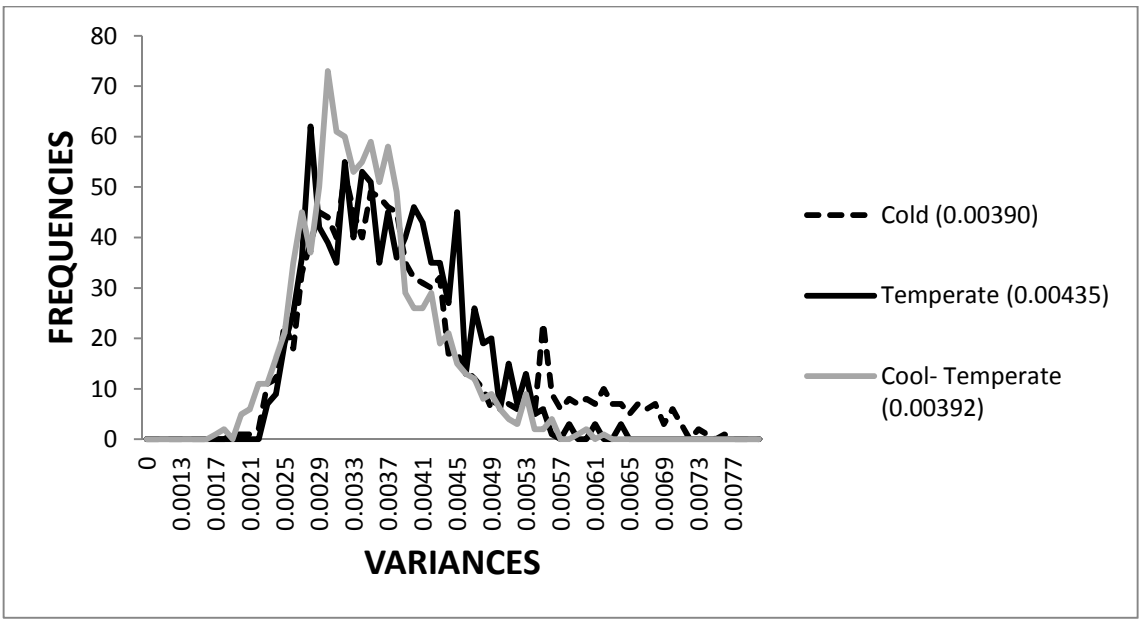

Figure 8.6: *Bootstrapped variance frequencies for M. subterraneus by climate at Westbury. Original variance values alongside corresponding value in the key.*

	Cold	Cool-Temperate
Cool-Temperate	**0.01513343**	
	0.538	
Temperate	**0.02320045**	**0.02308669**
	0.0097	*0.0295*

Table 8.14: *Results of Discriminant Function analysis of M. agrestis at Westbury by climatic conditions. Procrustes distances are shown in bold and associated p-values in italics.*

	Cold	Cool-temperate	Temperate
Cold	0.3500	0.3000	0.3500
Cool-temperate	0.2593	0.4815	0.2593
Temperate	0.2609	0.3623	0.3768

Table 8.15: *Results of a cross-validation analysis of M. agrestis from Westbury by climatic conditions. Values are shown as proportion of samples from a sample assigned to each sample.*

PC	Eigenvalues	% Variance	Cumulative %
1	0.00062227	16.64	16.64
2	0.00046710	12.49	29.13
3	0.00034140	9.13	38.26
4	0.00026183	7.00	45.26
5	0.00022550	6.03	51.29
6	0.00019446	5.20	56.49
7	0.00017357	4.64	61.13
8	0.00015406	4.12	65.25
9	0.00011889	3.18	68.43
10	0.00011582	3.09	71.52

PC	Eigenvalues	% Variance	Cumulative %
1	0.00117686	29.70	29.70
2	0.00046211	11.66	41.36
3	0.00030486	7.69	49.05
4	0.00026752	6.75	55.80
5	0.00023053	5.81	61.61
6	0.00015515	3.91	65.52
7	0.00013066	3.29	68.81
8	0.00011652	2.94	71.75
9	0.00010042	2.53	74.28
10	0.00009433	2.38	76.66

PC	Eigenvalues	% Variance	Cumulative %
1	0.00061904	16.85	16.85
2	0.00050661	13.79	30.64
3	0.00039658	10.80	41.44
4	0.00028142	7.66	49.10
5	0.00023373	6.36	55.46
6	0.00019062	5.19	60.65
7	0.00017432	4.74	65.39
8	0.00014531	3.95	69.34
9	0.00011325	3.08	72.42
10	0.00009638	2.62	75.04

Table 8.16 *First 10 Eigenvalues from PCA of M. agrestis (top), P. gregalodies (centre) and M. subterraneus (bottom) from Westbury.*

8.3.4: HYPOTHESIS 8.4- *THERE IS NO SIGNIFICANT CO-DEPENDENT, INTRASPECIFIC VARIATION IN BOTH SIZE AND SHAPE ACCORDING TO CLIMATE AT WESTBURY.*

As both size and shape have been shown to be statistically significant when attempting to identify differences in the M_1 in differing climatic conditions, this hypothesis attempts to combine both shape and size in Procrustes form space to see if further separation between climatic conditions can be achieved and more in-depth investigation of the difference in interspecific morphology can be observed.

Log Centroid sizes, as calculated during GPA are included with Procrustes-fitted coordinates in a PCA to maximise the amount of shape and size represented within the analysis. Eigenvalues can be seen in Table 8.16. Procrustes form-space diagrams for each species can be seen in figures 8.7-8.9. As can be seen from the PCA diagrams, there appears to be a large overlap between all three climatic conditions, with no clear separation between groups for each species. However, it can be seen that in all three species, specimens from cold conditions form a more tightly-constrained group, showing less variability in size or shape than samples from temperate or cool-temperate conditions.

In order to further explore the significance of any morphological changes caused by climatic conditions, cross-validation analyses are performed upon the Procrustes form space co-ordinates in order to evaluate if there is a significant difference between groups within each species dataset (tables 8.17, 8.18 and 8.19). In all three species, the cross-validation performs poorly, with less than 52% of specimens assigned to the correct group in all cases. These results do not represent an improvement when compared to the cross-validation results gained when size is excluded from the analyses, and therefore, it appears that size and shape do not co-vary according to climatic conditions.

On the basis of the evidence presented above, hypothesis 8.4 is rejected.

PC	Eigenvalues	% Variance	Cumulative %
1	0.002126	36.78	36.78
2	0.000589	10.18	46.96
3	0.000416	7.19	54.15
4	0.000339	5.86	60.01
5	0.000257	4.43	64.44
6	0.000231	3.99	68.43
7	0.000186	3.21	71.64
8	0.000179	3.09	74.73
9	0.000150	2.59	77.32
10	0.000119	2.05	79.37

PC	Eigenvalues	% Variance	Cumulative %
1	0.002440	37.37	37.37
2	0.001171	18.07	55.44
3	0.000471	7.27	62.71
4	0.000331	5.11	67.82
5	0.000274	4.22	72.04
6	0.000237	3.66	75.70
7	0.000162	2.49	78.19
8	0.000133	2.05	80.24
9	0.000122	1.89	82.13
10	0.000104	1.61	83.74

PC	Eigenvalues	% Variance	Cumulative %
1	0.001450	28.17	28.17
2	0.000598	11.98	40.15
3	0.000418	8.37	48.52
4	0.000373	7.48	56.00
5	0.000316	6.33	62.33
6	0.000245	4.90	67.23
7	0.000199	3.99	71.22
8	0.000166	3.32	74.54
9	0.000144	2.89	77.43
10	0.000115	2.30	79.73

Table 8.16: *First 10 Eigenvalues from PCA in Procrustes form-space of M. agrestis (top), P. gregalodies (centre) and M. subterraneus (bottom) from Westbury.*

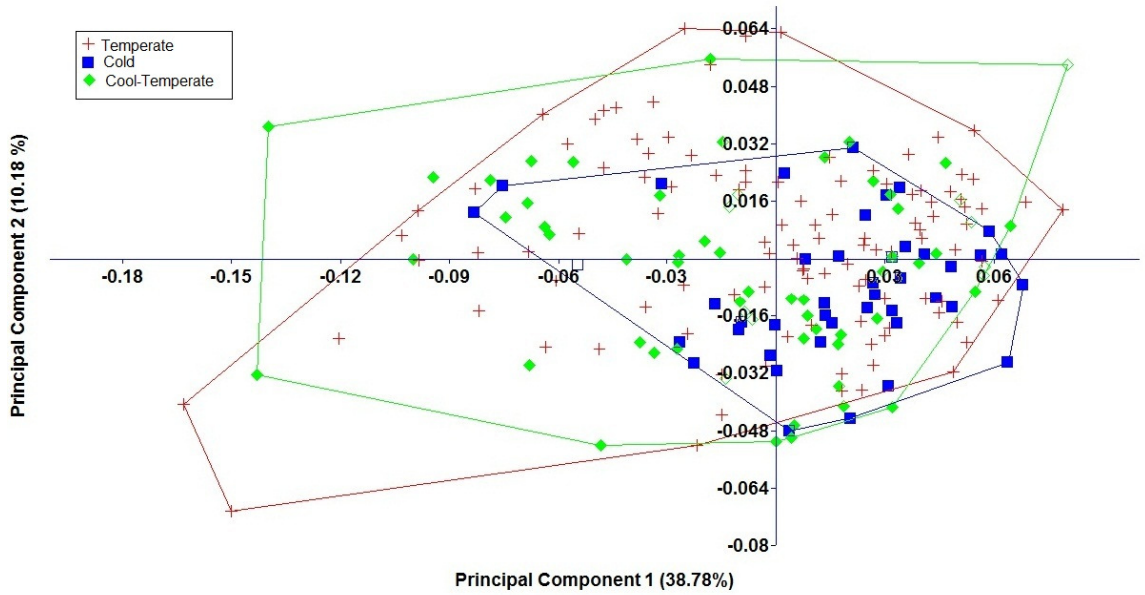

Figure 8.7: *Results of Principle Component analysis in Procrustes form space showing major axis of variation on PC1 and PC2 in the Westbury M. agrestis dataset on PC1 and PC2 by climate.*

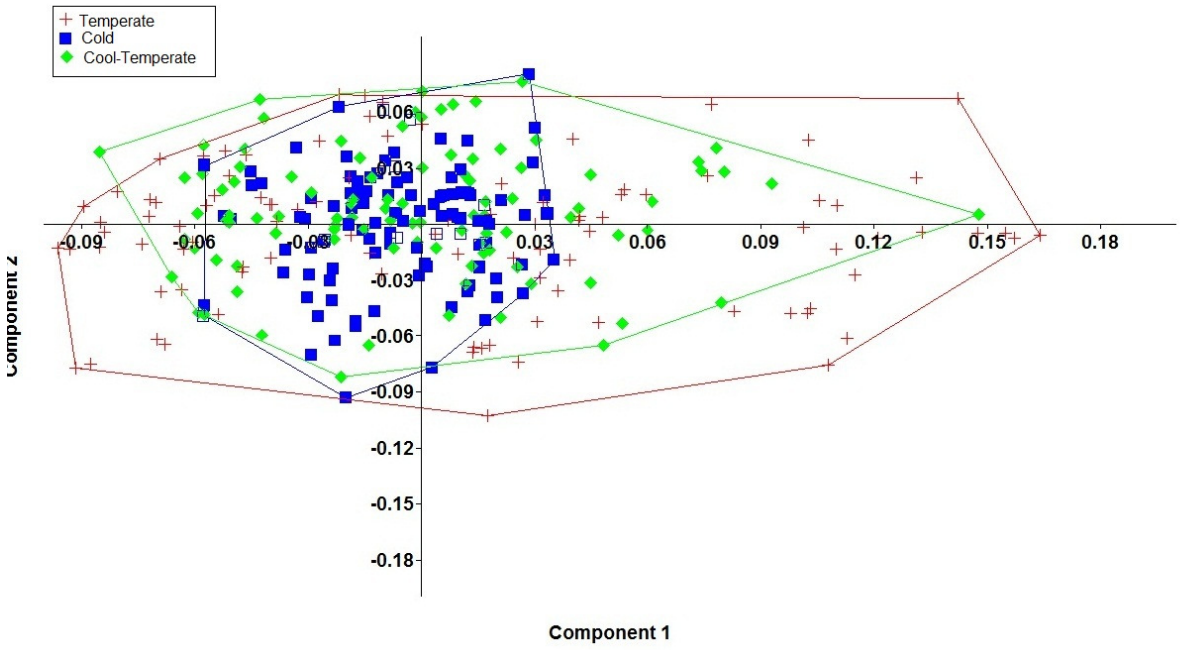

Figure 8.8: *Results of Principle Component analysis in Procrustes form space showing major axis of variation on PC1 and PC2 in the Westbury P. gregalodies dataset on PC1 and PC2 by climate.*

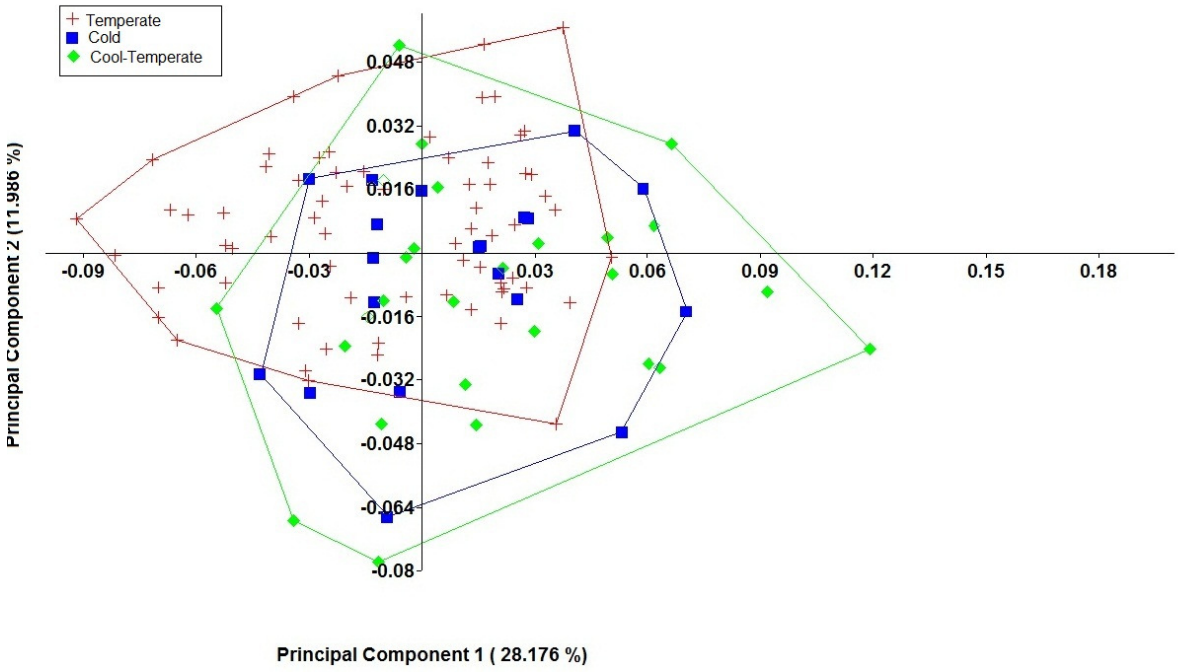

Figure 8.9: *Results of Principle Component analysis in Procrustes form space showing major axis of variation on PC1 and PC2 in the Westbury M. subterraneus dataset on PC1 and PC2 by climate.*

	Cold	Cool-temperate	Temperate
Cold	0.4651	0.2791	0.2558
Cool-temperate	0.3115	0.3770	0.3115
Temperate	0.4545	0.3273	0.2091

Table 8.17*: Results of a cross-validation analysis of M. agrestis from Westbury by climatic conditions. Values are shown as proportion of samples from a sample assigned to each sample.*

	Cold	Cool-temperate	Temperate
Cold	0.3714	0.3048	0.3238
Cool-temperate	0.3196	0.3711	0.3093
Temperate	0.3100	0.2900	0.4000

Table 8.18: *Results of a cross-validation analysis of P. gregalodies from Westbury by climatic conditions. Values are shown as proportion of samples from a sample assigned to each sample.*

	Cold	Cool-temperate	Temperate
Cold	0.3500	0.2500	0.3500
Cool-temperate	0.1852	0.5185	0.2963
Temperate	0.2464	0.3913	0.3913

Table 8.19: *Results of a cross-validation analysis of M. subterraneus from Westbury by climatic conditions. Values are shown as proportion of samples from a sample assigned to each sample.*

8.3.5. HYPOTHESIS 8.5*: THERE IS NO SIGNIFICANT INTRASPECIFIC VARIATION IN SIZE OF THE M_1 THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT WESTBURY.*

The centroid sizes are used in a Student's t-test to evaluate if the centroid sizes of samples from each stratigraphic level are significantly different.

Tables 8.20- 8.22 show the p-values obtained from the Students' t-test for each species. The results of the analyses show that there are significant differences in centroid size between specimens from some stratigraphic levels in all species present at Westbury. In *M. agrestis* and *M. subterraneus*, it appears that all unit 15 sub-units are similar in size, but are significantly different to all other stratigraphic levels. *P. gregalodies* shows very little significant differentiation in size throughout the sequence in comparison with the other two species. In order to investigate variation in size throughout the stratigraphic sequence at Westbury further, the mean sizes of specimens from each stratigraphic level sample are calculated. When these mean sizes are plotted, it is apparent that there is a consistent pattern in sample size throughout the stratigraphic sequence in all samples (Figure 8.10). The similarity in pattern between all species suggests that the pattern of significant results between stratigraphic levels is not influenced by sample size and therefore, must be caused by an external factor. Therefore, on the basis of the evidence presented above, hypothesis 8.5 is rejected.

	10	11	12	13	14	15-1	15-2	15-4	15-5	15-8	19-13
11	0.63657										
	0.5279										
12	-0.28023	-1.24473									
	0.7812	0.2183									
13	0.629935	0.012296	1.077806								
	0.5355	0.1122	0.2883								
14	-0.84637	-1.61742	-0.62443	-1.49391							
	0.4061	0.1122	0.5361	0.1464							
15-1	2.033742	1.302929	2.691509	1.159506	3.174327						
	0.0548	0.1989	0.0107	0.2568	0.0036						
15-2	2.353343	2.016799	3.538324	1.635717	3.834282	0.276467					
	0.024	0.048	0.0009	0.1094	0.0004	0.7835					
15-4	1.794312	1.464668	2.714668	1.189204	2.982818	0.057841	-0.2105				
	0.084	0.6553	0.0096	0.1094	0.0053	0.9542	0.8095				
15-5	0.093759	-0.44972	0.330045	-0.42087	0.745158	-1.46878	-1.83116	-1.38364			
	0.9266	0.6553	0.7437	0.6786	0.4644	0.1583	0.0966	0.1787			
15-8	-1.51108	-2.37908	-1.37383	-2.17603	-0.67461	-4.07843	-4.91043	-3.85522	-1.27038		
	0.1424	0.021	0.3536	0.037	0.5045	0.0003	<0.0001	0.0004	0.2156		
19-13	0.876555	0.370691	1.287709	0.318169	1.637696	-0.59498	-0.89224	-0.60822	0.610544	2.238961	
	0.3946	0.7128	0.2077	0.7537	0.1157	0.5585	0.3782	0.5483	0.552	0.0339	
19-14	-1.44649	-2.5663	-1.67782	-2.11052	-1.06245	-3.4144	-4.48515	-3.52788	-1.26089	-0.65847	-1.99332
	0.161	0.0133	0.1014	0.0436	0.2962	0.0019	<0.0001	0.0012	0.2206	0.5145	0.0582

***Table 8.20**: p-values from a Students' t-test on the M. agrestis dataset from Westbury sub-Mendip. Samples with significantly different means (p<0.05) are highlighted in yellow.*

	10	11	12	13	14	15/1	15/3	15/4	15/8	18	19/15
	-0.20588										
11	**0.8375**										
	-0.76956	*-0.46201*									
12	**0.444**	**0.6458**									
	-0.55084	*-0.2703*	*0.224093*								
13	**0.9963**	**0.7879**	**0.8233**								
	-0.80991	*-0.47874*	*0.046867*	*-0.20419*							
14	**0.4204**	**0.6338**	**0.9627**	**0.8388**							
	-1.38677	*-1.16432*	*-1.10072*	*-1.20451*	*-1.29051*						
15/1	**0.1725**	**0.2538**	**0.2776**	**0.2355**	**0.2035**						
	-1.43481	*-1.1694*	*-0.95652*	*-1.1195*	*-1.14309*	*0.423393*					
15/3	**0.1574**	**0.2499**	**0.3437**	**0.2686**	**0.2582**	**0.6773**					
	0.987619	*0.998818*	*1.439393*	*1.323916*	*1.624745*	*1.310691*	*1.740411*				
15/4	**0.3287**	**0.3261**	**0.1578**	**0.193**	**0.1112**	**0.2193**	**0.0999**				
	-2.0913	*-1.6711*	*-1.50532*	*-1.69008*	*-1.73562*	*0.200838*	*-0.33205*	*-1.98068*			
15/9	**0.0406**	**0.1013**	**0.1377**	**0.0964**	**0.0875**	**0.8423**	**0.7418**	**0.0575**			
	-0.52541	*-0.27424*	*0.15703*	*-0.04114*	*0.134841*	*1.053583*	*0.971511*	*-1.19751*	*0.214811*		
18	**0.6011**	**0.785**	**0.8757**	**0.9673**	**0.8931**	**0.3002**	**0.7418**	**0.2402**	**0.1499**		
	-1.23855	*-1.01113*	*-0.7788*	*-0.93756*	*-0.94635*	*0.53581*	*0.159198*	*-1.69063*	*0.461215*	*-0.81288*	
19/15	**0.2214**	**0.3191**	**0.4402**	**0.3535**	**0.3485**	**0.5999**	**0.875**	**0.1116**	**0.6477**	**0.4216**	
	-2.30732	*-1.86039*	*-1.60984*	*-1.83741*	*-1.88044*	*0.395112*	*-0.23243*	*-2.43479*	*1.462885*	*-1.59377*	*-0.41765*
20	**0.024**	**0.0683**	**0.1123**	**0.0707**	**0.0642**	**0.6952**	**0.8173**	**0.0201**	**0.8307**	**0.1166**	**0.6784**

Table 8.21: p-values from a Students' t-test on the P. gregalodies dataset from Westbury sub-Mendip. Samples with significantly different means (p<0.05) are highlighted in yellow.

	10	12	13	14	15/1	15/2	15/4
12	*1.592717*						
	0.1372						
13	*-0.3217*	-2.48266					
	0.7550	**0.0304**					
14	*0.603877*	*-1.15651*	*1.116151*				
	0.5572	**0.2668**	**0.2881**				
15/1	*3.327935*	*1.503316*	*4.716044*	*2.947183*			
	0.0034	**0.1470**	**0.0002**	**0.0075**			
15/2	*3.672588*	*2.055171*	*4.085785*	*3.356156*	*1.224007*		
	0.0007	**0.0460**	**0.0460**	**0.0017**	**0.2266**		
15/4	*3.944174*	*2.093181*	*4.951859*	*3.585381*	*0.842822*	*-0.62142*	
	0.0005	**0.0449**	**0.0449**	**0.0012**	**0.4046**	**0.5367**	
15/5	*2.594414*	*0.966465*	*3.679562*	2.22384	*-0.41328*	*-1.3929*	-1.13615
	0.0196	**0.3466**	**0.3466**	**0.0392**	**0.6828**	**0.1702**	**0.2638**

Table 8.22: *p-values from a Students' t-test on the M. subterraneus dataset from Westbury sub-Mendip. Samples with significantly different means (p<0.05) are highlighted in yellow, t-values are shown in italics.*

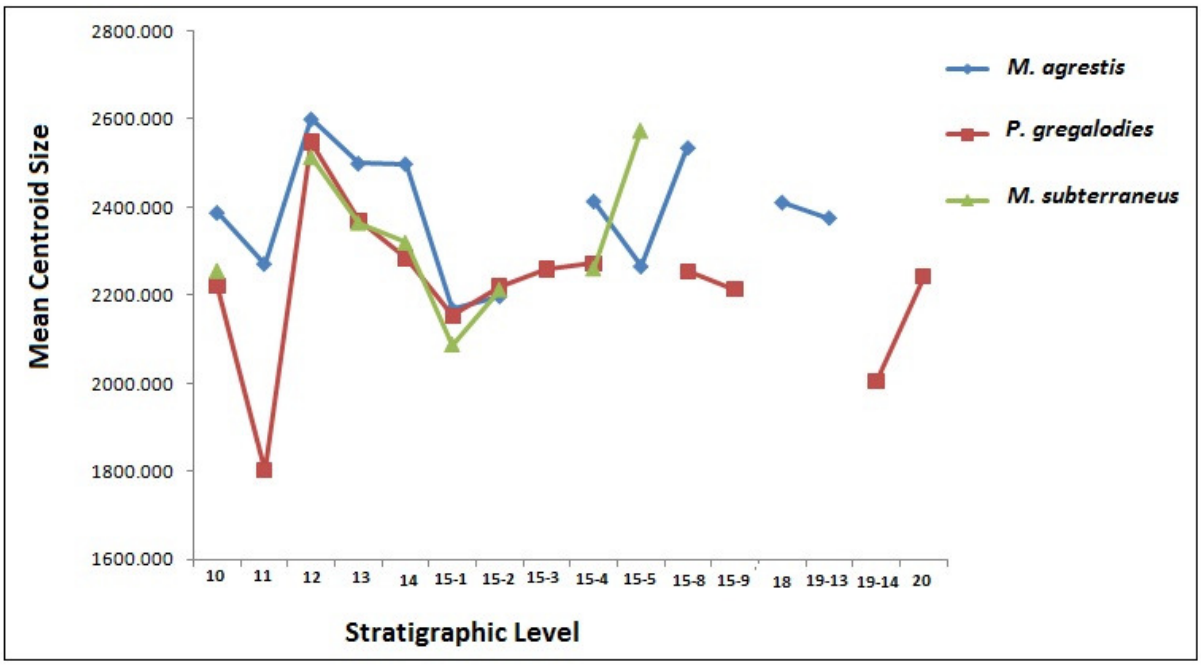

Figure 8.10: *Mean stratigraphic level centroid sizes of each species at Westbury.*

8.3.6 HYPOTHESIS 8.6- *THERE IS NO SIGNIFICANT INTRASPECIFIC VARIATION IN SHAPE OF THE LOWER M_1 THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT WESTBURY.*

In order to assess the degree of differentiation in shape between samples from different stratigraphic levels, principle components analysis is conducted on the Procrustes fitted data within each species. In all species, PC1, PC2 and all subsequent PCs the overlap between samples is too extensive to assess the degree of separation using principle components analysis. The Eigenvalue scores for the complete sample variance are given in table 8.16.

To provide further insight on the variation in morphology through the stratigraphic sequence, a discriminant function is run on each species dataset by stratigraphic level.

Tables 8.23-8.25 show the results of the Discriminant function analyses. For all species, there is a significant difference in the morphology of the M_1 in specimens from some stratigraphic levels. The significance between stratigraphic levels does not appear to be climate-driven, as some samples from the same climatic conditions are successfully discriminated. There appears to be no correlation between species as to the stratigraphic levels which are significantly different to one another, suggesting that the mechanisms driving this morphological change are intraspecific in nature. Figures 8.26-8.28 show cross-validation results for these samples, which perform poorly, with < 40 percent of all samples assigned to the correct group in all cases. The Mahalanobis distances are used to generate a dendrogram (calculated using UPGMA) for each species in order to provide a visual method of interpreting the relationships between stratigraphic levels at Westbury (Figures 8.11-8.13). These figures shown that, despite no correlation in the significance in morphological change through the stratigraphic levels between species, the relationship in Procrustes distances between species has a similar relationship in all cases, with sub-units from levels 15 and 19 plotting together separately from units 10-14. It is also shown that sub-units from within unit 15 are more similar to one another than to units 10-14, suggesting a relatively homogenous sample within this unit in all species.

Figures 8.14-8.15 show bootstrapped variance values within *M. agrestis* and *P. gregalodies* across stratigraphic levels (*M. subterraneus* sample sizes are considered to be too small to perform this type of analysis.) In both species, sub-unit 15-4 displays the highest original variance value, which might be expected as this level is a temperate level. However, there appears to be no clear increase invariance in levels with temperate conditions compared to those from cold within each species.

Results from this analysis have shown there is a significant difference in morphology between stratigraphic levels at Westbury, although the mechanisms driving this change are not clear. Therefore, on the basis of the results outlined above, hypothesis 8.3 is rejected

	10	11	12	13	14	15-1	15-2	15-4	15-5	15-8	19-13
11	0.0322 **0.2092**										
12	0.0292 **0.4328**	0.0137 **0.7223**									
13	0.0303 **0.9438**	0.0209 **0.0687**	0.0219 **0.3609**								
14	0.0201 **0.9706**	0.0243 **0.7223**	0.0222 **0.2002**	0.0218 **0.0623**							
15-1	0.0397 **0.9608**	0.0285 **0.0617**	0.0310 **0.0188**	0.0279 **0.4498**	0.0326 **0.7471**						
15-2	0.0396 **0.0073**	0.0296 **0.0002**	0.0295 **0.0527**	0.0268 **0.0040**	0.0345 **0.0434**	0.0229 **0.2958**					
15-4	0.0411 **0.6436**	0.0333 **0.0008**	0.0336 **0.1683**	0.0297 **0.3486**	0.0339 **0.6971**	0.0233 **0.9538**	0.0181 **0.6593**				
15-5	0.0529 **0.8719**	0.0436 **0.1351**	0.0439 **0.0894**	0.0523 **0.8054**	0.0517 **0.8196**	0.0511 **0.9600**	0.0430 **0.4585**	0.0436 **0.2292**			
15-8	0.0345 **0.3354**	0.0221 **0.2218**	0.0191 **0.5955**	0.0304 **0.3031**	0.0272 **0.8226**	0.0385 **0.2706**	0.0389 **0.0028**	0.0392 **0.1133**	0.0432 **0.4180**		
19-13	0.0438 **0.9853**	0.0355 **0.1224**	0.0338 **0.1196**	0.0332 **0.8077**	0.0413 **0.9484**	0.0275 **0.9773**	0.0266 **0.0637**	0.0287 **0.3655**	0.0459 **0.9943**	0.0355 **0.8770**	
19-14	0.0375 **0.6408**	0.0217 **0.0074**	0.0227 **0.0228**	0.0253 **0.3009**	0.0280 **0.2207**	0.0301 **0.1991**	0.0296 **0.0023**	0.0289 **0.1167**	0.0395 **0.6405**	0.0199 **0.016**	0.0298 **0.5844**

Table 8.23: *Results of Discriminant Function analysis of M. agrestis at Westbury by Stratigraphic level. Procrustes distances are shown in bold and associated p-values in italics. Statistically significant results (p=<0.05) are highlighted in yellow.*

	10	11	12	13	14	15-1	15-3	15-4	15-8	18	19-15
11	0.0285 **0.198**										
12	0.0292 **0.0081**	0.0193 **0.6529**									
13	0.0178 **0.1124**	0.0281 **0.1119**	0.0329 **0.0004**								
14	0.0189 **0.6278**	0.0259 **0.001**	0.0285 **<.0001**	0.0229 **0.1374**							
15-1	0.0306 **0.7036**	0.0302 **0.9658**	0.0346 **0.8842**	0.0244 **0.9752**	0.0353 **0.2213**						
15-3	0.0221 **0.2572**	0.03558 **0.7642**	0.0353 **0.0572**	0.0221 **0.1371**	0.026 **0.7627**	0.0292 **0.9119**					
15-4	0.0411 **0.9756**	0.0553 **0.9819**	0.0537 **0.8963**	0.0415 **0.8538**	0.05377 **0.8579**	0.0488 **0.9863**	0.054 **0.9186**				
15-8	0.0272 **0.2152**	0.0346 **0.0216**	0.0357 **0.0133**	0.028 **0.1316**	0.0225 **0.0113**	0.0397 **0.8596**	0.0848 **0.552**	0.0622 **0.7808**			
18	0.0145 **0.9613**	0.0238 **0.5118**	0.0275 **0.011**	0.0143 **0.1931**	0.0169 **0.1036**	0.0244 **0.9983**	0.0718 **0.8967**	0.0441 **0.9771**	0.0271 **0.0178**		
19-15	0.0366 **0.1018**	0.0438 **0.8661**	0.0456 **0.6811**	0.0329 **0.4658**	0.0296 **0.0421**	0.0449 **0.9687**	0.0841 **0.8414**	0.0616 **0.927**	0.0277 **0.9655**	0.0339 **0.8561**	
20	0.0372 **0.8538**	0.0386 **0.0001**	0.04212 **0.0002**	0.0357 **0.0125**	0.0258 **0.0017**	0.0477 **0.7009**	0.0934 **0.3404**	0.0707 **0.7537**	0.0191 **0.0525**	0.035 **0.0244**	0.0238 **0.9274**

Table 8.24: *Results of Discriminant Function analysis of P. gregalodies at Westbury by Stratigraphic level. Procrustes distances are shown in bold and associated p-values in italics. Statistically significant results (p=<0.05) are highlighted in yellow.*

	10	12	13	14	15/1	15/2	15/4
12	0.0521 **0.9874**						
13	0.0476 **0.9580**	0.0399 **0.9952**					
14	0.0308 **0.9987**	0.0445 **0.9988**	0.0367 **0.9985**				
15/1	0.0574 **0.9639**	0.0283 **0.8359**	0.0373 **0.8451**	0.0438 **0.8846**			
15/2	0.0585 **0.1141**	0.0320 **0.1142**	0.0359 **0.0265**	0.0437 **0.0169**	0.0238 **0.4273**		
15/4	0.07076447 **0.9479**	0.0540 **0.9882**	0.0509 **0.9774**	0.0543 **0.9117**	0.0481 **0.8171**	0.0324 **0.0283**	
15/5	0.0592 **0.988**	0.0310 **0.943**	0.0390 **0.9122**	0.0464 **0.9716**	0.0206 **0.0547**	0.0219 **0.6529**	0.0415 **0.7227**

Table 8.25 *Results of Discriminant Function analysis of M. subterraneus at Westbury by Stratigraphic level. Procrustes distances are shown in bold and associated p-values in italics. Statistically significant results (p=<0.05) are highlighted in yellow.*

	10	11	12	13	14	15-1	15-2	15-4	15-5	15-8	19-13	19-14
10	0.0000	0.1111	0.1111	0.1111	0.2222	0.2222	0.0000	0.0000	0.1111	0.1111	0.0000	0.0000
11	0.1471	0.2059	0.1765	0.1176	0.0294	0.0882	0.0000	0.0000	0.0294	0.1176	0.0000	0.0882
12	0.0417	0.1667	0.2083	0.1250	0.1250	0.0000	0.0000	0.0833	0.0833	0.0833	0.0000	0.0833
13	0.0000	0.2857	0.1429	0.2143	0.0000	01429	0.0714	0.0000	0.0000	0.0714	0.0000	0.0714
14	0.3125	0.0000	0.1250	0.0625	0.1875	0.0625	0.0000	0.0000	0.0625	0.1250	0.0000	0.0625
15-1	0.1429	0.0000	0.0714	0.0000	0.0000	0.2143	0.1429	0.1429	0.0714	0.0714	0.0714	0.0714
15-2	0.0333	0.0667	0.1000	0.1000	0.0333	0.1000	0.1333	0.3333	0.0333	0.0000	0.0667	0.0000
15-4	0.0000	0.0000	0.0000	0.1000	0.0500	0.0000	0.2500	0.2000	0.1000	0.0500	0.1500	0.1000
15-5	0.2857	0.0000	0.0000	0.2857	0.1429	0.0000	0.0000	0.2857	0.0000	0.0000	0.0000	0.0000
15-8	0.1000	0.0000	0.0000	0.1000	0.0500	0.0000	0.0500	0.0000	0.0500	0.4000	0.0500	0.2000
19-13	0.0000	0.2500	0.0000	0.0000	0.1250	0.1250	0.0000	0.2500	0.0000	0.0000		0.2500
19-14	0.0000	0.0000	0.0000	0.0588	0.0000	0.0588	0.0000	0.1176	0.0588	0.2941	0.1176	0.2941

Table 8.26: *Results of a cross-validation analysis of M. agrestis from Westbury by stratigraphic level. Values are shown as proportion of samples from a sample assigned to each sample*

	10	11	12	13	14	15-1	15-2	15-3	15-4	15-8	18	19-13	19-15	20
10	0.1282	0.0769	0	0.1282	0.1538	0.0513	0.0256	0.0256	0.1795	0.0513	0.0513	0.0256	0.0513	0.0513
11	0.16	0.2	0.12	0	0.08	0	0.12	0.04	0	0.16	0.08	0	0.04	0
12	0.1667	0	0.2222	0.0556	0.1111	0.0556	0.1389	0	0.0278	0.0833	0.0833	0.0278	0.0278	0
13	0.2222	0.0833	0.1111	0.1389	0.1667	0.0556	0.0278	0.0833	0	0.0556	0	0.0278	0	0.0278
14	0.0732	0.0732	0.0732	0.1463	0.1951	0.0732	0	0.0488	0.122	0.0976	0.0732	0.0244	0	0
15-1	0.1667	0	0	0.1667	0	0	0.1667	0.3333	0	0.1667	0	0	0	0
15-2	0	0	0	0	0	0.5	0.5	0	0	0	0	0	0	0
15-3	0	0	0	0.2308	0.1538	0	0.2308	0.3846	0	0	0	0	0	0
15-4	0	0.1667	0	0	0	0.1667	0	0.5	0.1667	0	0	0	0	0
15-5	0.0833	0	0.125	0	0	0.0417	0	0.125	0.0833	0.2083	0.125	0.0417	0.125	0.0417
18	0.1111	0.1852	0.037	0.0741	0.1481	0	0.1111	0.037	0.0741	0.1111	0.037	0	0	0.0741
19-13	0.5	0	0	0	0	0	0	0	0	0	0.5	0	0	0
19-15	0	0	0.1818	0	0	0.2727	0	0.4545	0.0909	0	0	0	0	0
20	0.0645	0.1613	0	0	0.0323	0.0968	0.129	0.1935	0.0645	0.0323	0.0645	0.0968	0.0323	0.0323

Table 8.27: *Results of a cross-validation analysis of P. gregalodies from Westbury by stratigraphic level. Values are shown as proportion of samples from a sample assigned to each sample.*

	10	12	13	14	15-1	15-2	15-4	15-5
10	0.1667	0.5000	0.0000	0.0000	0.1667	0.1667	0.0000	0.0000
12	0.0000	0.2500	0.1250	0.1250	0.0000	0.1250	0.1250	0.1250
13	0.2000	0.0000	0.4000	0.0000	0.2000	0.0000	0.2000	0.0000
14	0.2500	0.1250	0.1250	0.1250	0.0000	0.1250	0.2500	0.0000
15-1	0.1250	0.0625	0.1875	0.0625	0.2500	0.1250	0.1250	0.0625
15-2	0.0000	0.2703	0.0811	0.1351	0.0541	0.2162	0.0811	0.1622
15-4	0.1250	0.1667	0.0833	0.1250	0.0833	0.0417	0.1250	0.2500
15-5	0.0000	0.0000	0.2500	0.0833	0.1667	0.0000	0.1667	0.3333

Table 8.28: *Results of a cross-validation analysis of M. subterraneus from Westbury by stratigraphic level. Values are shown as proportion of samples from a sample assigned to each sample.*

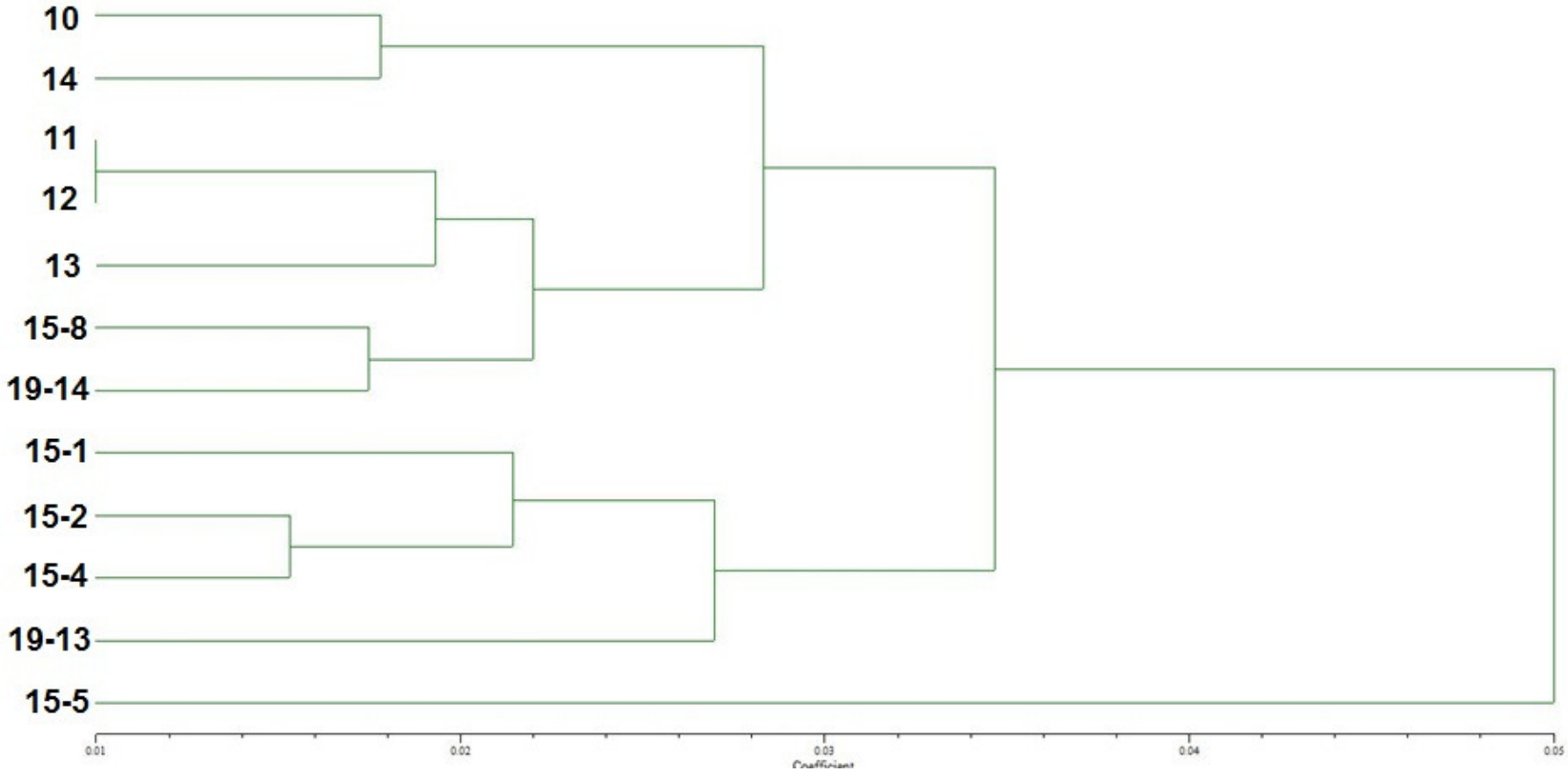

Figure 8.11: *UPGMA tree calculated using Mahalanobis distances illustrating relationships between the shapes of M. agrestis M_1 teeth throughout the stratigraphic sequence at Westbury.*

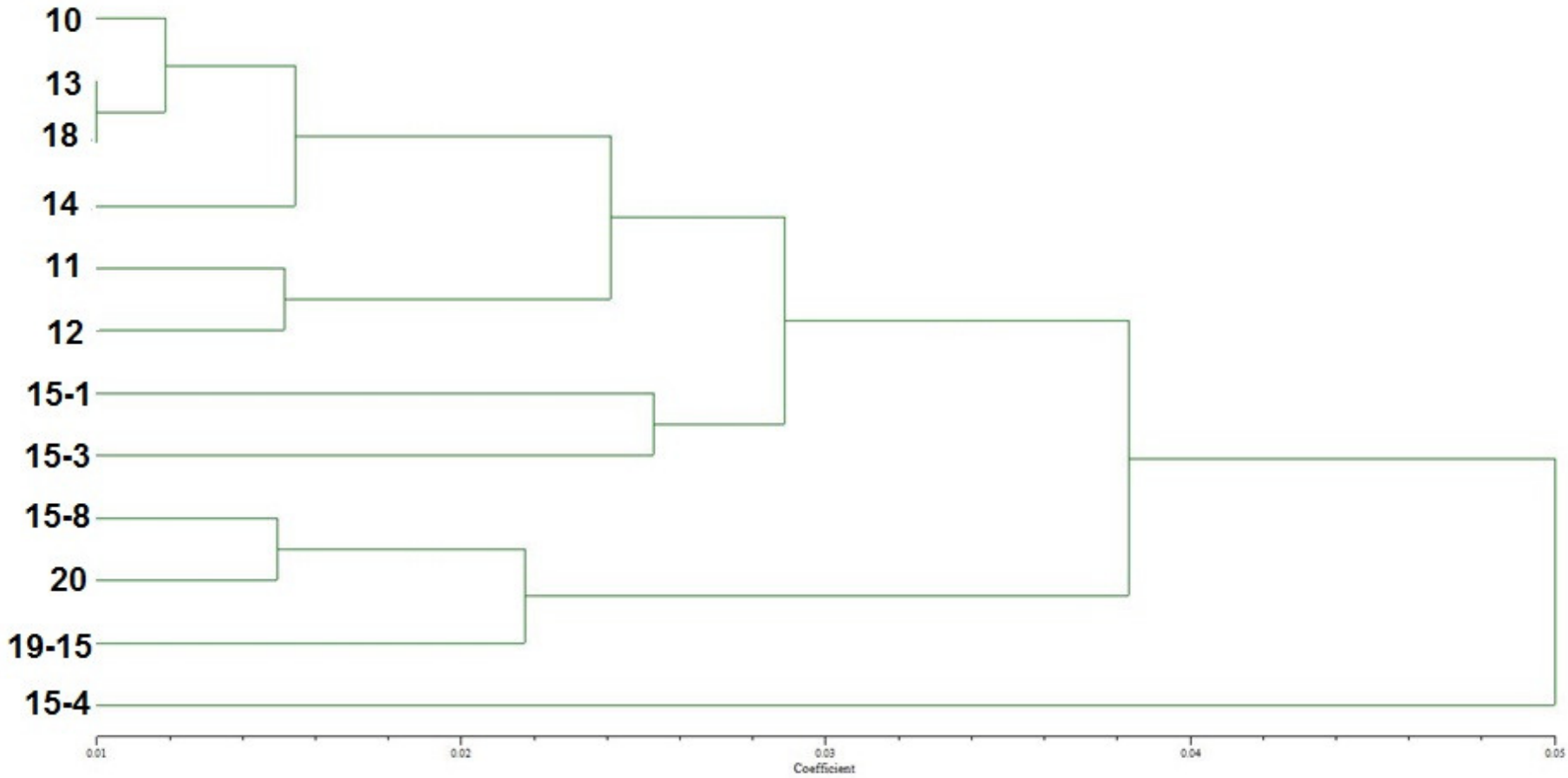

Figure 8.12: *UPGMA tree calculated using Mahalanobis distances illustrating relationships between the shapes of P. gregalodies M_1 teeth throughout the stratigraphic sequence at Westbury.*

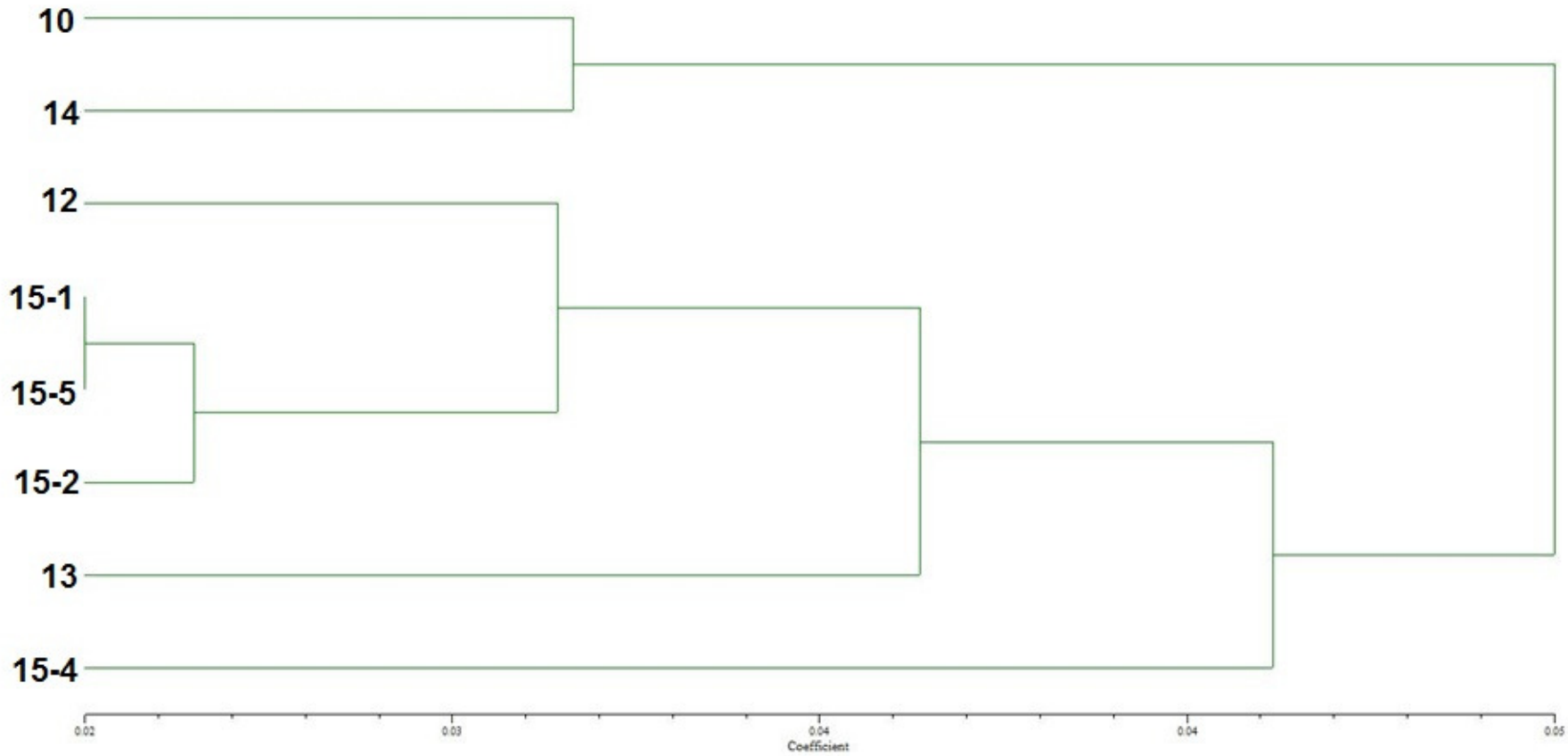

Figure 8.13: *UPGMA tree calculated using Mahalanobis distances illustrating relationships between the shapes of M. subterraneus M_1 teeth throughout the stratigraphic sequence at Westbury.*

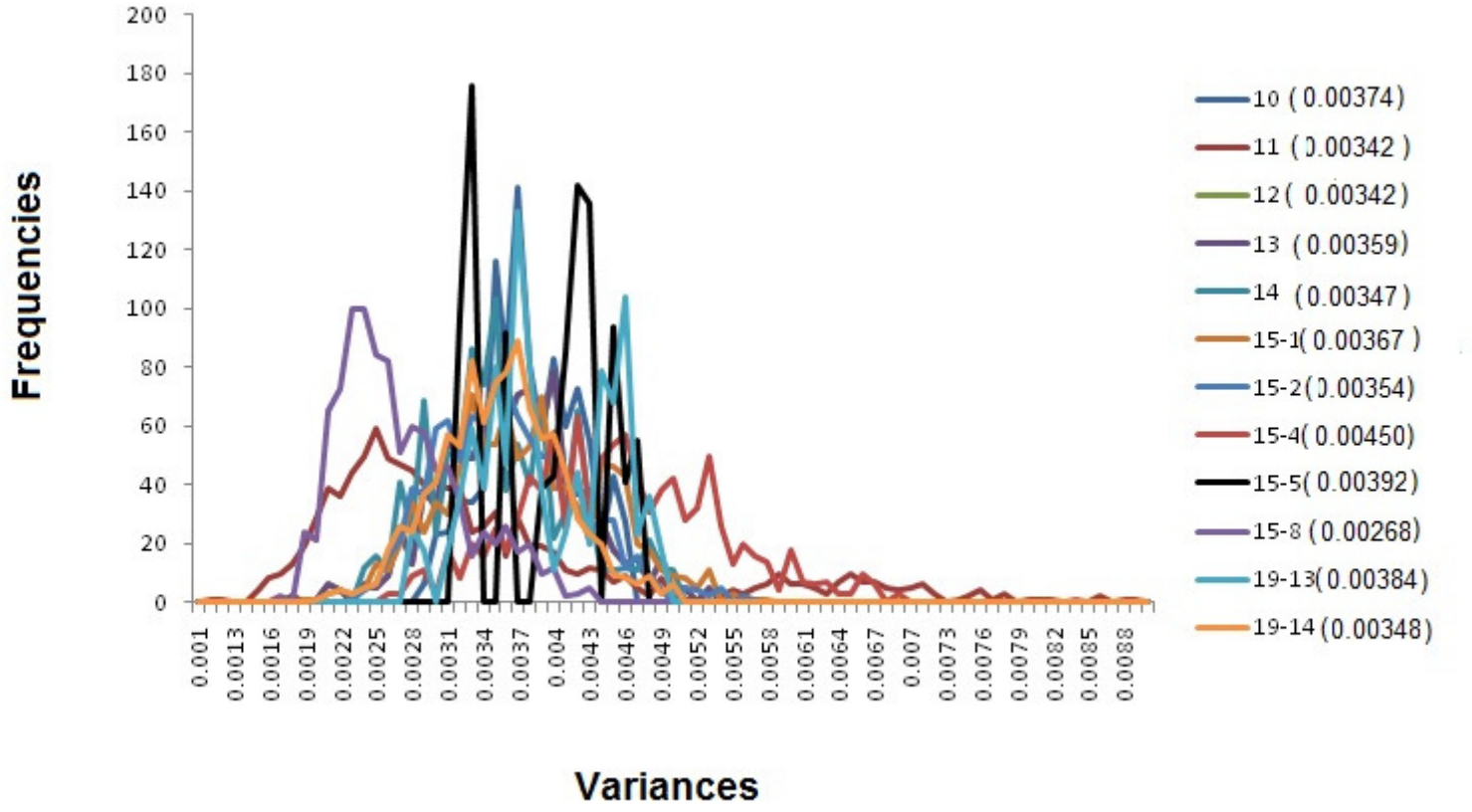

Figure 8.14: *Bootstrapped variance frequencies for M. agrestis by stratigraphic level at Westbury. Original variance values alongside corresponding value in the key.*

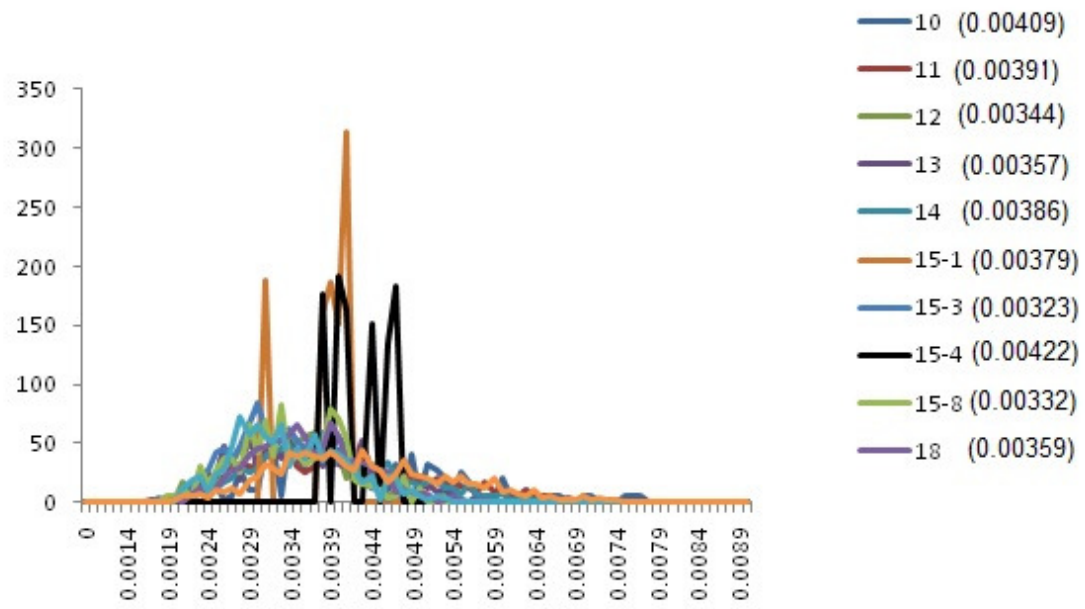

Figure 8.15: *Bootstrapped variance frequencies for P. gregalodies by stratigraphic level at Westbury. Original variance values alongside corresponding value in the key.*

8.3.7 HYPOTHESIS 8.7: *THERE IS NO SIGNIFICANT INTRASPECIFIC, CO-DEPENDANT VARIATION IN BOTH SIZE AND SHAPE OF MICROTUS LOWER M_1 THROUGHOUT THE STRATIGRAPHIC SEQUENCE AT WESTBURY.*

Figures 8.16-8.18 show PCA of *M. agrestis*, *P. gregalodies* and *M. subterraneus* in Procrustes form-space. As can be seen from these diagrams, there is very little clear separation between stratigraphic levels observed in PC1 and PC2 across the entire sample. Tables 8.29-8.31 show that, when samples are submitted to cross-validation analyses, the ability of the cross validation to assign samples correctly is very poor (< 40% in all cases). These results provide no significant improvement over results gained in section 8.3.6 and therefore suggest that both size and shape do not co-vary throughout the stratigraphic sequence at Westbury. On the basis of this evidence, hypothesis 8.7 cannot be rejected.

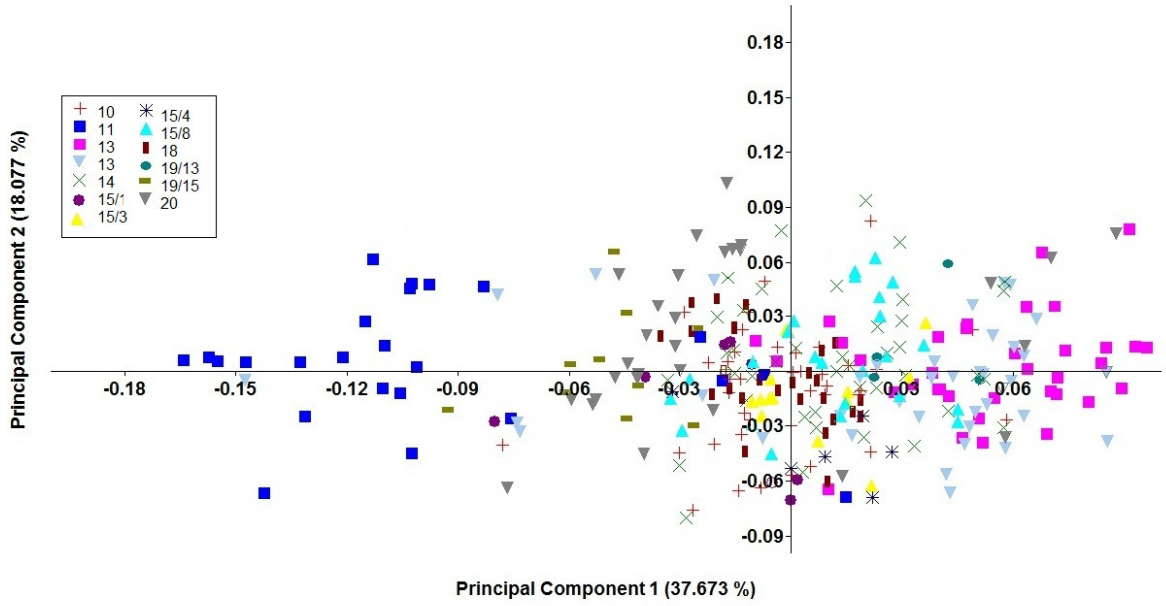

Figure 8.16: *Results of Principle Component analysis in Procrustes form space showing major axis of variation on PC1 and PC2 in the Westbury M. agrestis dataset on PC1 and PC2 by stratigraphic level.*

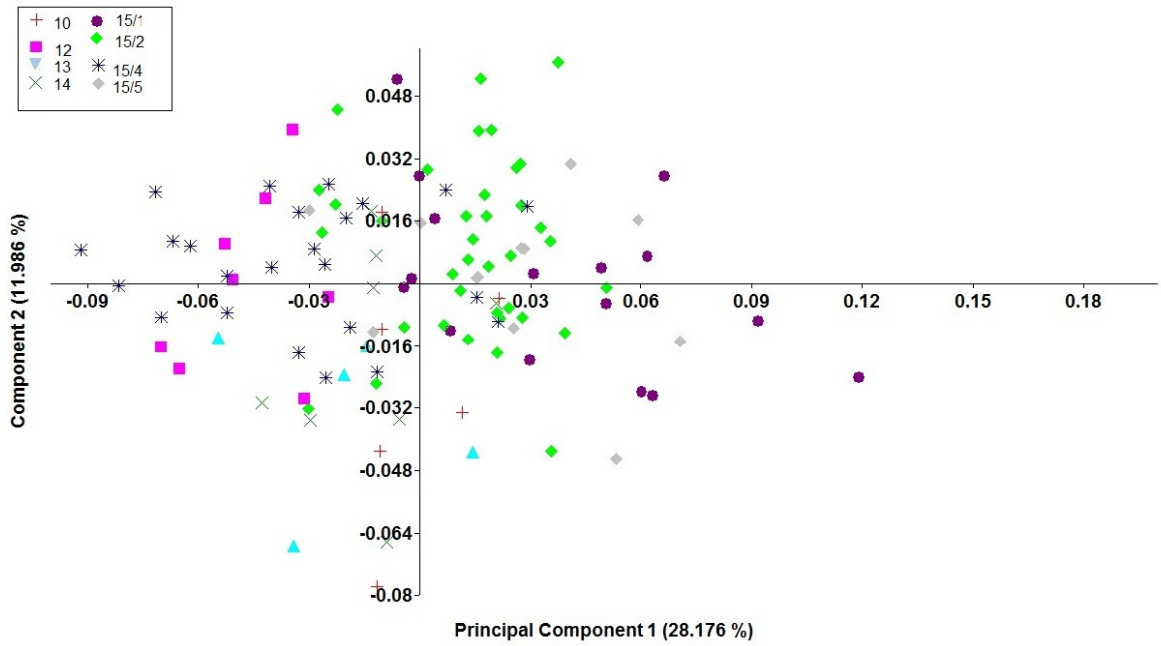

Figure 8.17: *Results of Principle Component analysis in Procrustes form space of showing major axis of variation on PC1 and PC2 in the Westbury P. gregalodies dataset on PC1 and PC2 by stratigraphic level.*

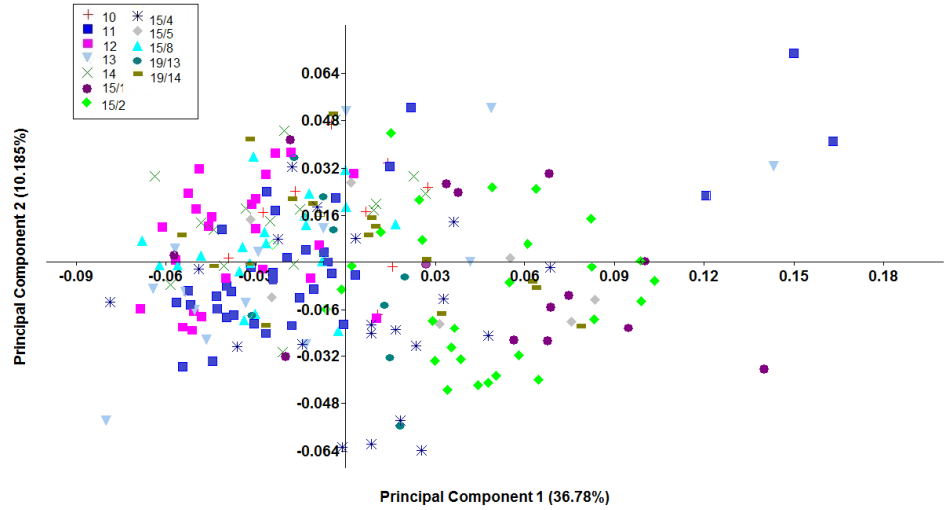

Figure 8.18: Results of Principle Component analysis in Procrustes form space of showing major axis of variation on PC1 and PC2 in the Westbury M. subterraneus dataset on PC1 and PC2 by stratigraphic level.

	10	11	12	13	14	15-1	15-2	15-4	15-5	15-8	19-13	19-14
10	0	0.111	0	0.1111	0.4444	0.222	0	0	0	0.111	0	0
11	0.1471	0.206	0.147	0.1176	0.0294	0.065	0.065	0	0.029	0.088	0.029	0.088
12	0.0417	0.125	0.375	0.0833	0.125	0	0	0.042	0.042	0.083	0	0.083
13	0	0.214	0.143	0.2143	0	0.071	0	0.143	0.071	0.071	0	0.071
14	0.2857	0	0.071	0.0714	0.2143	0.071	0	0	0	0.143	0	0.143
15-1	0.0714	0	0	0	0	0.214	0.286	0.071	0.143	0	0.143	0.071
15-2	0.0667	0.067	0	0.0667	0.0667	0.067	0.3	0.2	0.133	0	0.033	0
15-4	0	0	0.05	0.1	0.1	0	0.25	0.2	0.05	0.05	0.15	0.05
15-5	0	0.143	0.143	0	0	0.143	0.286	0.286	0	0	0	0
15-8	0.1	0.05	0.05	0.05	0.05	0	0	0.05	0.05	0.4	0.05	0.15
19-13	0	0.25	0	0	0	0.25	0	0.25	0	0	0	0.25
19-14	0	0	0	0.0588	0	0.118	0.059	0.118	0.059	0.294	0.059	0.235

Table 8.29: *Results of a cross-validation analysis of M. agrestis from Westbury by stratigraphic level in Procrustes form-space. Values are shown as proportion of samples from a sample assigned to each sample.*

	10	11	12	13	14	15-1	15-2	15-3	15-4	15-8	18	19-13	19-15	20
10	0.1026	0.0513	0.0000	0.0769	0.1282	0.0513	0.1026	0.0256	0.1795	0.0256	0.0513	0.0769	0.0513	0.0769
11	0.0000	0.1600	0.1200	0.2400	0.0800	0.0800	0.0000	0.0000	0.0400	0.1200	0.0800	0.0000	0.0800	0.0000
12	0.0833	0.0278	0.2222	0.1111	0.1111	0.0833	0.0000	0.0278	0.0278	0.0556	0.0833	0.0769	0.0833	0.0278
13	0.1667	0.1389	0.1111	0.1389	0.1944	0.0556	0.0278	0.0556	0.0000	0.0833	0.0000	0.0000	0.0000	0.0278
14	0.0732	0.0000	0.0732	0.2439	0.2195	0.0000	0.0000	0.0244	0.1220	0.0976	0.1220	0.0244	0.0000	0.0000
15-1	0.1667	0.0000	0.0000	0.1667	0.0000	0.0000	0.1667	0.3333	0.0000	0.1667	0.0000	0.0000	0.0000	0.0000
15-2	0.0000	0.0000	0.0000	0.0000	0.0000	0.5000	0.5000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
15-3	0.0000	0.0000	0.0000	0.2308	0.1538	0.0000	0.2308	0.3846	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
15-4	0.0000	0.1667	0.0000	0.0000	0.0000	0.1667	0.0000	0.5000	0.1667	0.0000	0.0000	0.0000	0.0000	0.0000
15-8	0.0833	0.0000	0.1250	0.0000	0.0000	0.0417	0.0000	0.1250	0.0833	0.2083	0.1250	0.0417	0.1250	0.0417
18	0.1111	0.1852	0.0370	0.0741	0.1481	0.0000	0.1111	0.0370	0.0741	0.1111	0.0370	0.0000	0.0000	0.0741
19-13	0.5000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.5000	0.0000	0.0000	0.0000
19-15	0.0000	0.0000	0.1818	0.0000	0.0000	0.2727	0.0000	0.4545	0.0909	0.0000	0.0000	0.0000	0.0000	0.0000
20	0.0645	0.0323	0.2258	0.0645	0.0645	0.0000	0.0968	0.0323	0.0323	0.0968	0.1290	0.1613	0.0000	0.0000

Table 8.30: *Results of a cross-validation analysis of P. gregalodies from Westbury by stratigraphic level in Procrustes form-space. Values are shown as proportion of samples from a sample assigned to each sample.*

	10	12	13	14	15-1	15-2	15-4	15-5
10	0.3333	0.1667	0.0000	0.3333	0.0000	0.1667	0.0000	0.0000
12	0.2500	0.3750	0.1250	0.1250	0.0000	0.0000	0.1250	0.0000
13	0.2000	0.0000		0.6000	0.2000	0.0000	0.0000	0.0000
14	0.0000	0.0000	0.2500	0.2500	0.0000	0.1250	0.2500	0.1250
15-1	0.0000	0.3750	0.1250	0.0625	0.2500	0.1250	0.0625	0.0000
15-2	0.0811	0.1351	0.0811	0.0811	0.2162	0.1622	0.1351	0.1081
15-4	0.1250	0.1667	0.0833	0.1250	0.0833	0.0417	0.1250	0.2500
15-5	0.0000	0.0833	0.1667	0.0833	0.1667	0.0833	0.1667	0.2500

Table 8.31: *Results of a cross-validation analysis of M. subterraneus from Westbury by stratigraphic level in Procrustes form-space. Values are shown as proportion of samples from a sample assigned to each sample.*

8.4 DISCUSSION

Within the Westbury dataset, a relatively low proportion of allometry is observed in all three *Microtus* species. In both M. *subterraneus* and P. *gregalodies* datasets, the percentage of shape variance explained by size is considered to be statistically insignificant (1.24 and 0.42 percent respectively). The allometric component to the M. *agrestis* dataset is found to be slightly higher at 2.5674 percent, which is considered statistically significant ($p < 0.0001$). The amount of allometry found within the Westbury dataset is slightly lower than that observed in the smaller Walou Cave and Boxgrove samples, which, in turn, are smaller than that found in the Modern dataset. The reason for the decreased allometry within the Westbury dataset in comparison to the other archaeological datasets may be explained by the increased size of these samples, and the large degree of shape variance within the samples. Innes et

al.,(1995) and McGuire (2009) have also observed an allometric component to datasets of other *Microtus* species. However, in both cases, it is still possible to correlate the shape of M_1 teeth with climatic and environmental variables independently of size. Similar shape changes are observed in all species; as the size of the tooth increases, the anteroconid complex (AC) becomes proportionally smaller and relatively tilted towards the buccal surface of the tooth. Re-entrant angles 4 and 5 also become less pronounced. This relative shortening and increased curvature of the AC region suggest that the majority of size change within the teeth may come from T1-T5, which is surprising, as this has traditionally been considered to be a less plastic region of the tooth than the AC region (e.g.; Hinton, 1923; Gutherie, 1965; Van der Meulen, 1976).

When the Westbury material is examined in the context of climatic changes throughout the sequence, significant differences between warm and cold levels are seen on both a large and small scale. When all samples from stratigraphic levels with similar climatic reconstructions (Andrews, 1999) are combined and analysed for differences in size between groups, results of a Students' t-test show that, for all species, a statistically significant difference in size between cold and temperate groups is found. Samples from cold stratigraphic levels are shown to be larger than those from temperate conditions. The finding is in agreement with Bergmann's rule, which states that species living in cold conditions will become larger as a mechanism to conserve heat loss (Bergman, 1847). However, it is in disagreement with studies published by Nadachowski (1984) and Mointure and Brunet-Lecomte (2004), who found that in *Microtus nivalis* and *Microtus Grafi* respectively, the opposite relationship is found, with tooth size increasing slightly in warmer conditions.

However, in both studies, no strong correlation between tooth size and climatic conditions is found, unlike in this study, where results are highly statistically significant.

When the effect of climate upon morphological variability within the Westbury *Microtus* faunas is tested, no immediate difference between samples from different climatic conditions can be seen in PCA data. However, discriminant function analyses of the same datasets suggests there is a highly statistically significant net difference in morphology between samples from temperate stratigraphic levels and those from both cold and cool-temperate levels in all species. All species display an increase in the tilt of the AC region and T4 and T5 towards the lingual surface of the tooth in warmer conditions. When the relative variance of the climatic samples is considered, it is shown that, in all species, samples from warmer climatic conditions have increased variance as compared to those which come from cooler conditions, with cold conditions displaying the lowest amount of variance within the samples. The same pattern of decreased variance is also seen within Procrustes form-space analyses of the same material. This decrease in variance within cold conditions is also observed within the Boxgrove dataset and may be due to several factors. Under warmer climatic conditions, resources are likely to increase, leading to decreasing interspecific competition for resources. This could allow either a new morphology to be expressed *in situ* or could lead to increased population sizes and therefore, increased genetic mixing between populations (Nadachowski, 1984; Spears & Clarke, 1987; Mointure & Brunet-Lecomte, 2004). Therefore, it is suggested that although climate is not likely to have a direct effect upon M_1 morphology, its effects on factors such predation, competition, maturation rate and mixing between populations may indirectly influence the amount of shape variance seen in the M_1.

The fact that a clear climatic signal can be seen in both size and shape of *Microtus* M_1 teeth at Westbury suggests that the affect of climate upon the teeth of *Microtus* is both independent from and strong enough to overcome the allometric component within the datasets. This finding, along with those of Mointure and Brunet-Lecomte (2004) and McGuire (2009), suggests that an important implication of this finding is the potential for *Microtus* species to be used as a palaeoclimatic proxy in addition to standard methods of analysis such as the Mutual Climatic Range theory in beetles and molluscs (e.g. Moine et al., 2002; Elias, 2001) and climatic reconstruction using habitat preferences of mammalian species (e.g. Andrews, 1990).

Throughout the Westbury dataset, variation in the size and shape of teeth is strongly correlated with climatic variables (discussed in detail below) and, therefore, it suggests that the climatic signals within the Westbury dataset are a strong determinate of shape variability within the data despite the allometric component. This supposition is supported by the fact that when climatic samples are analysed in Procrustes form space, where both shape and size are included, the strength of cross-validation analyses to assign specimens to the correct climatic group does not increase when compared to samples performed on Procrustes-fitted co-ordinates with variation in size excluded.

When the variance in M_1 size and morphology throughout the stratigraphic sequence at Westbury is analysed, the pattern of variation between samples is not as clear as when climatic variables are analysed. Results of students' t-tests on centroid size show that, within all species, there are some significant differences in size between stratigraphic levels. *M. agrestis and P. gregalodies* datasets show a broad pattern in

that units 10-14 have no significant difference in size, but are significantly different from all sub-units from units 15 and 19. Sub-units within unit 15 and unit 19 show no difference in size. Very little variance in size in the *M. subterraneus* dataset is observed. However, when the mean sizes of each species at each stratigraphic level are plotted, it can be seen that the trend in increased or decreased size throughout the stratigraphic sequence is similar for all three *Microtus* species. The fact that all three species display the same pattern in size throughout the stratigraphic sequence suggests that the trends shown are not an artefact of sample sizes. There appears to be some influence of climate within the dataset, but this does not explain all of the observed size change. The exact mechanism for this size change is currently unclear, although it may be linked to biological factors such as increased pressure on food resources due to increased inter-specific competition or increased predation (e.g. Yoccoz & Rolf, 1999; Getz et al., 1987).

When Morphological changes within the M_1 throughout the stratigraphic sequence are evaluated, a similar pattern to that observed with size variance is observed. Units 10-13 are more similar in morphology to those from unit 15 and higher and significant differences in morphology are observed between several stratigraphic levels. The fact that little significant difference is found in size or shape in unit 15 sub-units may be of archaeological importance. As outlined in chapter 2, excavation at Westbury took place in several different locations due to difficulties in gaining access to the sediments (Andrews & Cook, 1999). Therefore, the correlation between sedimentary units excavated at different sites is not always clear. Sub-units15-1 and 15-3 are thought to represent lateral extremes of the same unit, based upon lithological and faunal analysis, as are sub-units 15-2 and 15-4. No evidence is found within these analyses to

suggest that these units are not contemporaneous and they are closely linked to other unit 15 sub-units, based on their similarity in morphology and size. Analysing samples in Procrustes form-space does not improve the ability of cross-validation analyses to distinguish between stratigraphic samples, suggesting that size and morphology vary independently of one another throughout the sequence.

8.5 CONCLUSIONS

- There is a significant allometric component to *M. agrestis*, *P. gregalodies* and *M. subterraneus* at Westbury sub-Mendip; however, this allometry does not appear to be caused by change in size over time or climate.
- *Microtus* M_1 teeth are significantly larger in specimens from contexts representing colder conditions than those from warmer conditions.
- *Microtus* M_1 teeth of all species included within this study show significant changes in morphology as the climate cools, with specimens becoming more tilted towards the AC region in all species.
- As the climate cools, the morphological variance observed within each sample is reduced in comparison with specimens from warmer levels.
- There are also significant changes in size and morphology of *Microtus* M_1 teeth between some stratigraphic levels at Westbury, which does not appear to be linked to climatic change, suggesting genetic factors may be responsible.

CHAPTER 9
THE TAXONOMY OF EARLY MIDDLE PLEISTOCENE *MICROTUS* AND THE RELATIVE AGES OF WESTBURY AND BOXGROVE

The British early Middle Pleistocene record is made up of several geographically and temporally disparate sites, as discussed in detail in chapter 1 of this thesis. The age of these sites means that they are not suitable for many absolute dating techniques, such as C^{14} dating. Where appropriate absolute dating techniques have been attempted using methods such as Thermoluminescence, amino acid racemisation and Uranium series dating, although there is often no correlation in the dates obtained using different techniques, as demonstrated at Boxgrove, possibly as these techniques are being used close to their limits (e.g. Parks & Rendell, 1999; Rhodes, 1999; Sykes, 1999). As a result, in sites of this period age determination is more commonly based upon indirect, often relative techniques such as biostratigraphy and lithostratigraphy

The sites of Westbury and Boxgrove are important within the British Early Middle Pleistocene record and a clear understanding their relative ages is key to the understanding of this period in Britain and Europe.

As discussed in chapter 1, both sites have complex stratigraphic sequences and are believed to represent more than one climatic phase. The faunal remains from both

sites suggest that they fall within the Cromerian Complex, and while they are similar to each other they are distinct from both older Cromerian assemblages (which contain *Mimomys)* and younger Anglian faunas (see chapter 1 for detailed discussion of the biostratigraphic significance of mammalian faunas). There has been debate as to the relative ages of Westbury and Boxgrove; Schreve (1999) has suggested that Westbury and Boxgrove are of approximately the same age (one or more warm peaks in MIS 13) based upon the similarity in their faunal assemblages, although Parfitt and Preece (2000) have argued that the presence of the archaic *P. gregalodies* at Westbury suggests it is older than Boxgrove and possibly dates to MIS 15.

In fossil material, species are identified on the basis of morphological similarity with extant species. This reliance on morphological characteristics can be problematic, as a similarity in morphology may not necessarily represent a shared evolutionary history. However, the ability of GMM methods to distinguish between modern species and sub-species of *Microtus*, based on M_1 morphology, is extremely robust, as demonstrated in chapter 4 of this volume. The Westbury and Boxgrove datasets are particularly suitable for detailed analysis as they provide large sample sizes from well-understood stratigraphic locations. The four main aims of this chapter (discussed in more detail below) are proposed in order to gain further insight into both the evolutionary divergence of modern *Microtus* species since the Early Middle Pleistocene and, also to evaluate the relative age of Westbury and Boxgrove. The aims of this chapter are as follows;

1) **To evaluate the degree of morphological variation between archaeological datasets and modern samples and, on the basis of this evidence, to examine**

and suggest revisions to the taxonomic relationship between archaeological and modern samples.

Microtus species are known to have evolved extremely rapidly over the Quaternary period. This rapid evolution makes it possible to use morphological change in the dentition of *Microtus* species as a biostratigraphic tool. The use of geometric morphometric methods to identify significant morphological differences between species and populations has been demonstrated in chapter 5. Therefore, it may be possible to identify significant differences between archaeological 'species' and modern species.

Therefore, on the basis of the evidence presented above, the following hypotheses are erected:

Hypothesis 9. 1: *There is no significant difference in morphology between modern and early Middle Pleistocene specimens of the same species.*

Hypothesis 9. 2- *There is no significant difference in M_1 size between modern and early Middle Pleistocene Microtus M_1 of the same species.*

2) To evaluate the degree of similarity in morphology between species from Westbury sub-Mendip and Boxgrove, in relation to the relative ages of the sites.

The relative ages of Westbury sub-Mendip and Boxgrove, and their position within the Cromerian complex have been matters for debate in the literature. Relative dating techniques have proved inconclusive at both sites (See Rea, 1999; Parks & Rendell, 1999; Rhodes, 1999; Grün, 1999, Currant, 1999 for further details). Therefore, the

mammalian remains have proved to be the most useful indicator of age at the sites (Parfitt & Roberts, 1999; Current, 1999). Schreve et al., (1999) have suggested that there is a correlation between the small mammal faunas of units 11 and 15/2, 15/4 at Westbury and unit 4c at Boxgrove. Both mammal assemblages are very similar and have been interpreted as representing interglacial conditions followed by a marked cooling period and are suggested to belong to Cromerian interglacial IV.

However, Parfitt and Preece (2000) claim that the presence of abundant *P. gregalodies* remains at Westbury and *M. gregalis* at Boxgrove strongly suggest that the temperate deposits at Westbury are older than those at Boxgrove and belong to Cromerian interglacials III and IV respectively (potentially correlating with MIS 15 and MIS 13).This would mean there is a significant age difference between the two sites in that evolutionary changes can occur in rapidly-evolving *Microtus* species (as suggested by the *P. gregalodies*/ *M. gregalis* transition). Geometric Morphometric analysis of all *Microtus* species will be used to investigate the variability in shape between the same species at both sites. If the samples are found to be significantly different, this will support the suggestion that the sites are of a different age. Therefore, the following hypotheses are erected;

Hypothesis 9.3: *There is no difference in species composition at Boxgrove and Westbury sub-Mendip.*

Hypothesis 9.4: *Samples from Boxgrove and Westbury-sub Mendip have no significant difference in morphology through time.*

3) Establishing the relative positions of Middle Pleistocene sites

As discussed above, the position of both Westbury and Boxgrove in the Cromerian Complex is debated. Comparison of the morphology of Westbury and Boxgrove *Microtus* faunas with those from other Middle Pleistocene sites may give a clearer picture of the age of both sites in relation to other Cromerian sites. If the samples are shown to be statistically significantly different from sites that are thought to belong to different Cromerian temperate stages, the potential for *Microtus* M_1 teeth to be used as a non-absolute dating technique in providing correlations between sites exists. Therefore, the following hypotheses are erected;

Hypothesis 9.5: *Specimens from Boxgrove and Westbury will have no significant difference in morphology to those from the Middle Pleistocene sites at Cudmore Grove and West Runton.*

If samples from Westbury and Boxgrove are truly the same age, samples should show no significant difference to one another, but differ significantly to samples from both younger and older sites.

9.2 MATERIAL AND METHODS

9.2.1 MATERIAL

The datasets used in these analyses are composed of a total of 1103 specimens of *M. agrestis, M. arvalis, M. gregalis, M. subterraneus* and *P. gregalodies.* The samples include the modern dataset (as described in detail in chapter 4), Boxgrove (chapter 6), Westbury (chapter 8) and a dataset made up of samples from several other sites of Cromerian age as detailed in Table 9.1. All samples are of whole, undamaged adult teeth, including examples from both left and right-hand sides. These samples are chosen for these analyses as they allow for comparison between archaeological and modern M_1 morphologies, including extant species. Twenty-five landmarks are collected from each tooth, as described in chapter 3, comprising 15 fixed landmarks and 10 semi-sliding landmarks along the curve of the AC region.

	M. agrestis	***M. arvalis***	***M. gregalis***	***M. subterraneus***
Modern	96	45	100	118
Boxgrove	50	18	4	41
Westbury	217	-	352	119
Cudmore Grove	19	-	-	-
West Runton	25	-	-	-

Table 9.1: *Summary of number of specimens per species at each site included in this chapter.*

9.2.2 METHODS

In all analyses, landmarks are firstly superimposed using Generalised Procrustes Analysis (GPA) to remove variation due to translation and rotation and to separate shape from size. In all samples, specimens recorded as *M. arvalis*/ *M. agrestis* due to the isolated nature of the M_1 teeth (and lack of associated M^2) are assigned to the species using the discriminant function methodology used in previous chapters.

When looking at the difference in morphology between stratigraphic levels at Westbury and Boxgrove, *M. agrestis* and *M. subterraneus* are chosen as the only species suitable for this analysis. The reasons for this selection are two-fold: Firstly, *M. gregalis* is present in only very small numbers at Boxgrove (4 specimens) and therefore analyses based on stratigraphic levels are not possible, as the sample sizes are too small and do not cover a sufficient stratigraphic range. Secondly, on the basis of the discriminant function analyses, *M. arvalis* is not present at Westbury. This finding has important implications that are presented and discussed in hypothesis 2. Further analyses within each hypothesis are as follows;

H 9.1: Principal Components Analyses (PCA) are performed using the Procrustes-fitted coordinates from the GPA to visualise the major axes of variation in the dataset. In order to investigate the variation within the datasets further, a discriminant function with cross-validation is then performed using the Mahalanobis D^2 distances between group means. To visualise the relative distances between groups, the unweighted pairgroup method using arithmetical averages (UPGMA) is used to produce phenographic trees showing relationships between species, explained in chapter 3. The UPGMA trees are calculated using the Procrustes distances between species datasets. All UPGMA trees are calculated using the landmark methodology on the basis of the full set of landmarks, as shown in chapter 3. Diagrammatic visualisations of the mean shape of each sample are calculated using thin plate splines. In order to compare the variance within samples, variance in each group is calculated from the Procrustes fitted coordinates of all specimens within that group. A range of variance values is then calculated via bootstrapping the original data 1000 times. The bootstrap values are

then plotted to provide curves illustrating the distribution of variance in shape-space for each sample.

H 9.2: A Students' t-test is performed on the centroid sizes of each sample, as calculated during the Procrustes fit of the combined samples.

H 9.3: Archaeological samples of *M. arvalis/ agrestis* (including the *M. arvalinus* morphotype) are assigned to the correct species based upon their morphological distance from modern samples, as calculated in a discriminant function analysis, as described in chapter 3.

H 9.4 and H9.5: A Principal Components Analysis (PCA) is performed using the Procrustes-fitted coordinates from the GPA to visualise the major axes of variation in the dataset. In order to further investigate the variation in the datasets, a discriminant function with cross-validation is then performed using the Mahalanobis D^2 distances between group means. To visualise the relative distances between groups, the unweighted pairgroup method using arithmetical averages (UPGMA) is used to produce phenographic trees showing relationships between species, explained in chapter 3. The UPGMA trees are calculated using the Procrustes distances between species datasets. All UPGMA trees are calculated using the landmark methodology on the basis of the full set of landmarks, as shown in chapter 3.

9.3 RESULTS

9.3.1 HYPOTHESIS 9.1: THERE IS NO SIGNIFICANT DIFFERENCE IN MORPHOLOGY BETWEEN MODERN AND EARLY MIDDLE PLEISTOCENE SPECIMENS OF THE SAME SPECIES.

In order to create a summary of the major axes of variation in the sample, Procrustes fitted landmark co-ordinates for all samples are used to calculate a co-variance matrix that is then subjected to Principal Components Analysis. Figure 9.1 shows the results of the Principal Components Analysis of all modern, Westbury sub-Mendip and Boxgrove specimens. PC 1 and PC 2 combined count for 37.562 percent of the overall variance observed in the sample. The associated Eigenvalues for all Principal Components are shown in table 9.2.

As can be seen from the PCA diagram (Figure 9.1), modern and archaeological specimens of the same species tend to be more similar in morphology to one another than to other species. *M. agrestis* and *M. arvalis* samples inhabit a very similar position in morphospace, however, there is a clear separation of *M. subterraneus* and *M. gregalis* samples. There is also a clear separation between the *M. gregalis* sample from Boxgrove and Modern samples and the Westbury *P. gregalodies* samples, which is to be expected given the distinctive morphology of *P. gregalodies*. The Modern *M. subterraneus* sample is also clearly differentiated from all other samples. All modern species appear to have a wider distribution than their Early Middle Pleistocene counterparts. This pattern of separation is easily observed throughout the first 10 principal components, that together account for 78.009 % of the overall shape variation observed in the sample.

PC	Eigenvalues	% Variance	Cumulative %
1	0.00120843	23.64	78.18
2	0.00071377	13.94	54.54
3	0.00054472	10.54	40.60
4	0.00045412	8.87	30.06
5	0.00026084	5.09	21.19
6	0.00024017	4.98	16.10
7	0.00016955	3.31	11.12
8	0.00015248	2.97	7.81
9	0.00012710	2.48	4.84
10	0.00012084	2.36	2.36

Table 9.2: *First 10 Eigenvalues for PC analysis of all datasets including percentage of variation within the whole dataset explained by each PC and cumulative percentage.*

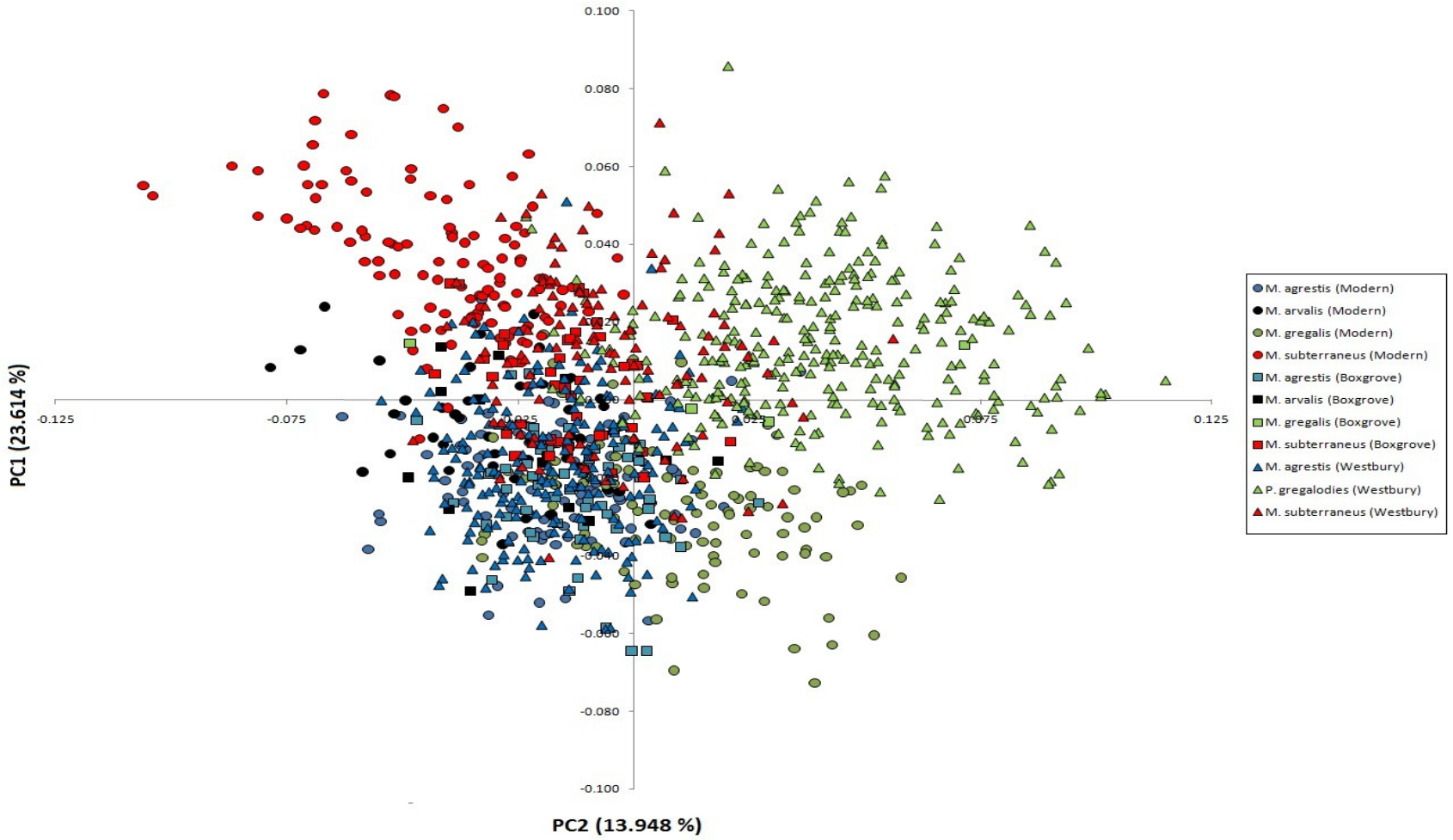

Figure 9.1: *Results of Principle Component analysis in showing major axis of variation in modern, Boxgrove and Westbury datasets on PC1 and PC2 by stratigraphic level.*

As can be seen in table 9.3, discriminant function analysis shows a highly statistically significant difference in M_1 morphology between all samples, including all specimens of all species. Procrustes distances between samples suggest that most specimens of the same species are more similar morphologically than they are to those of other species. *M. subterraneus* samples from the modern dataset are distinct from all other specimens, including Westbury and Boxgrove *M. subterraneus*. Cross-validation results based on the discriminant function analysis (Table 9.4) show that when specimens are treated as unknown, they could be correctly assigned to the correct group > 80 percent of the time in all samples, with the exception of *M. gregalis* from Boxgrove. The lower degree of correctly assigned specimens in this sample is likely to be an artefact of the very small sample size (4 individuals). Many of the samples can be correctly identified > 95 percent of the time. Therefore, an extremely robust and distinct separation in morphology between modern and archaeological samples of all species is confirmed.

In order to visualise the relationship of Procrustes distances between samples, a UPGMA tree is constructed. As can be seen in figure 9.2, for all species Westbury and Boxgrove samples are more similar morphologically to one another than they are to the modern samples. This result is not surprising, as Westbury and Boxgrove are thought to be similar in age to one another, approximately 500, 000 years older than the modern samples.

The overall structure of the relationships summarised in the UPGMA tree also reflect the genetic relationships found in modern species, where *M. arvalis* and *agrestis* are the most closely related species, followed by *M. subterraneus* and *M. gregalis* being more distantly related. This suggests that the morphology of *Microtus* teeth may have

a strong genetic component. However, as can be seen in figure 9.2, the position of modern *M. subterraneus* samples is separate from all other samples and widely convergent from Westbury and Boxgrove samples. This separation is unlikely to be an artefact of sample size, as all samples are greater than 40 individuals.

In order to investigate this further, the bootstrapped variance values for modern and archaeological *M. subterraneus* samples are calculated and are presented in figure 9.3. The original variance values for the modern sample are approximately the same size as those found at Westbury, however both modern and Westbury samples have significantly greater variance than the Boxgrove sample. This is not surprising, given the restricted geographical range and temporal range of the Boxgrove sample when compared to the modern sample and Westbury sample respectively. Table 9.5 shows variance values of all samples and species, and in all cases variance is reduced in the Boxgrove sample.

Figure 9.4 illustrates the difference in morphology for each species between datasets, in relation to the mean shape of all specimens of the species from all datasets.

On the basis of the evidence presented above, H1 is rejected.

	M. agrestis Boxgrove	*M. agrestis* Modern	*M. agrestis* Westbury	*M. arvalis* Boxgrove	*M. arvalis* Modern	*M. gregalis* Boxgrove	*M. gregalis* Modern	*M. subterraneus* Boxgrove	*M. subterraneus* Modern	*M. subterraneus* Westbury
M. agrestis Modern	0.03274812									
	<.0001									
M. agrestis Westbury	0.0266317	0.04667728								
	<.0001	<.0001								
M. arvalis Boxgrove	0.04406922	0.0526438	0.03607778							
	<.0001	<.0001	<.0001							
M. arvalis Modern	0.04434531	0.0511625	0.03055167	0.02869527						
	<.0001	0.012	<.0001	0.0009						
M. gregalis Boxgrove	0.05394595	0.06438271	0.05037932	0.05920339	0.05593572					
	<.0001	<.0001	<.0001	<.0001	<.0001					
M. gregalis Modern	0.0593648	0.05944254	0.06310032	0.05200571	0.05800531	0.05120131				
	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001				
M. subterraneus Boxgrove	0.05640712	0.06427869	0.05261828	0.03559832	0.0496861	0.06301865	0.06051777			
	<.0001	<.0001	<.0001	0.003	<.0001	<.0001	<.0001			
M. subterraneus Modern	0.08113109	0.09013203	0.07086032	0.06274678	0.05987224	0.09626425	0.1005189	0.06139288		
	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001		
M. subterraneus Westbury	0.05815478	0.06676023	0.04672556	0.06274678	0.04762838	0.05941321	0.06199658	0.03469961	0.06320946	
	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	
M. subterraneus Westbury	0.0693803	0.06676023	0.06259428	0.05769242	0.06510109	0.05314194	0.05943274	0.04209109	0.08287877	0.03192816
	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001

Table 9.3 : Results of Discriminant Function analysis of Modern, Boxgrove and Westbury datasets by species. Procrustes distances are shown in bold and associated p-values in italics.

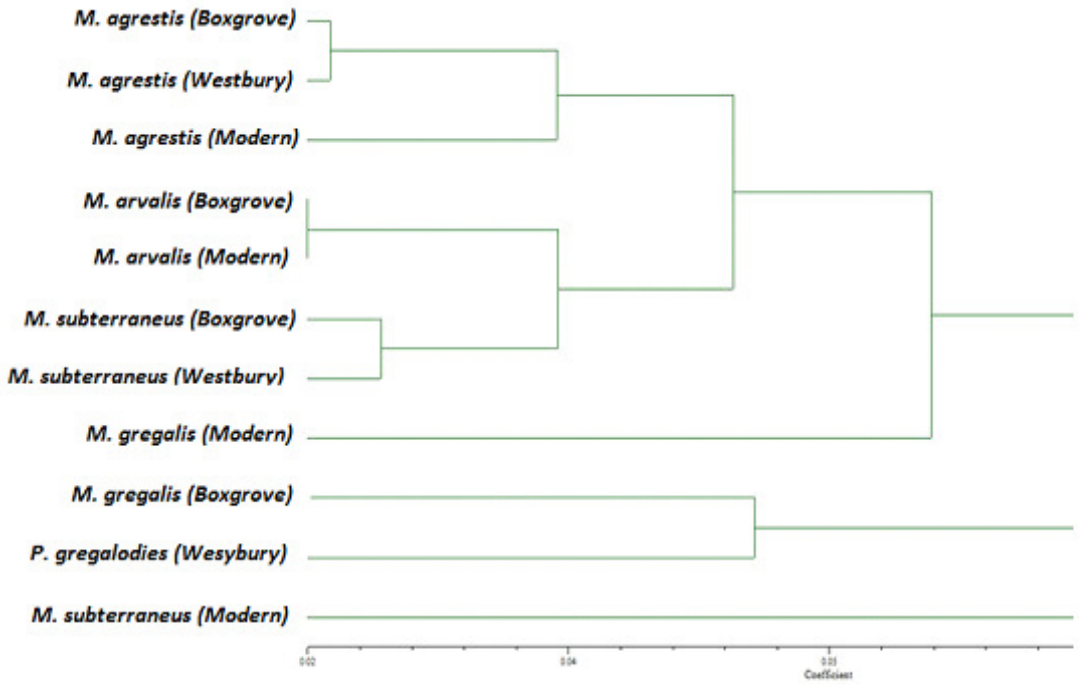

Figure 9.2: UPGMA tree showing relationships between samples based upon Procrustes distances.

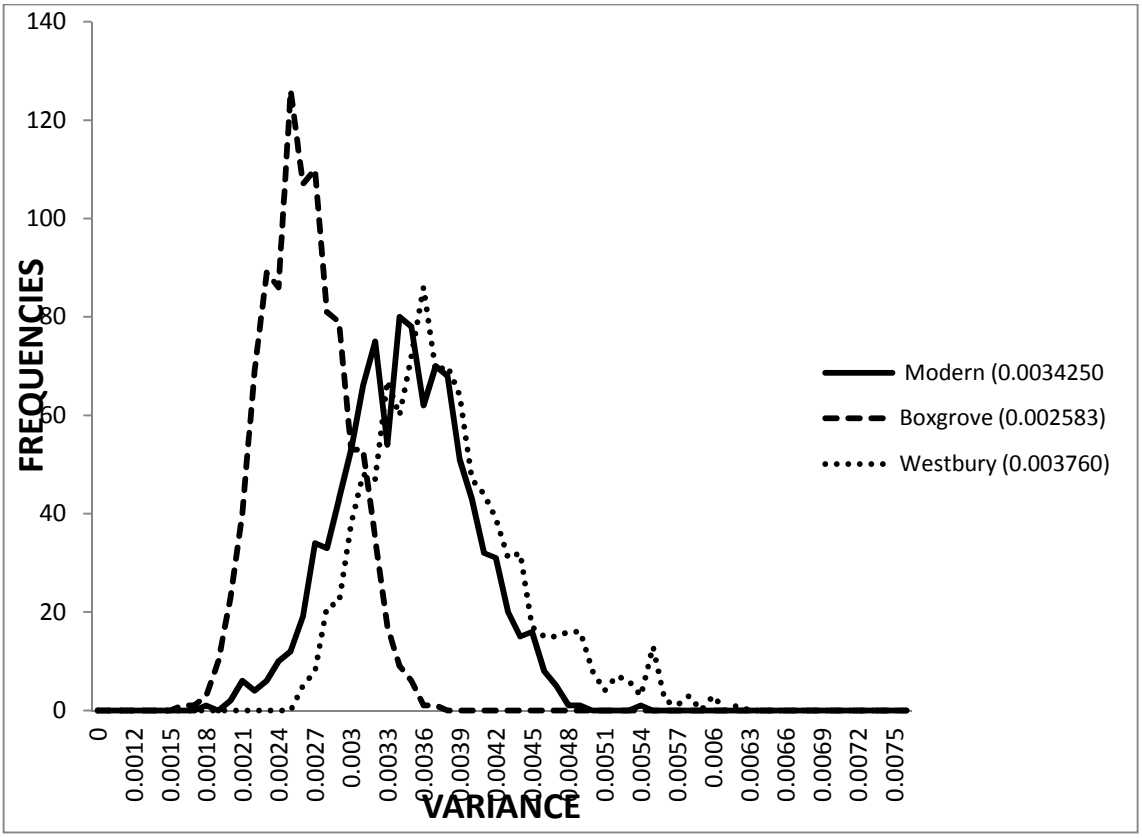

Figure 9.3: Bootstrapped variances of M. subterraneus from Modern, Boxgrove and Westbury datasets. Original variance values are shown alongside the corresponding group in the key.

	M. agrestis			*M. arvalis*		*M. gregalis*			*M. subterraneus*		
	Modern	Boxgrove	Westbury	Modern	Boxgrove	Modern	Boxgrove	Westbury	Modern	Boxgrove	Westbury
M. agrestis Modern	0.87	0.09	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. agrestis Boxgrove	0.04	0.90	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. agrestis Westbury	0.01	0.04	0.92	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. arvalis Modern	0.02	0.00	0.00	0.89	0.09		0.00	0.00	0.00	0.00	0.00
M. arvalis Boxgrove	0.14	0.00	0.00	0.14	0.86	0.00	0.00	0.00	0.00	0.00	0.00
M. gregalis Modern	0.00	0.00	0.00	0.00	0.00	0.86	0.11	0.03	0.00	0.00	0.00
M. gregalis Boxgrove	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
M. gregalis Westbury	0.00	0.00	0.00	0.00	0.00	0.00	0.97	0.03	0.00	0.00	0.00
M. subterraneus Modern	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.01
M. subterraneus Boxgrove	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.91	0.10
M. subterraneus Westbury	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.05	0.88

Table 9.4: Results of a cross-validation analysis of Modern, Boxgrove and Westbury datasets by species. Values are shown as proportion of samples from a sample assigned to each sample.

	Modern	Boxgrove	Westbury
M. agrestis	0.003648	0.003075	0.003771
M. gregalis	0.005271	0.004038	0.004189
M. subterraneus	0.003425	0.002583	0.003760

Table 9.5: *Original variance values for all species samples from Modern, Boxgrove and Westbury datasets.*

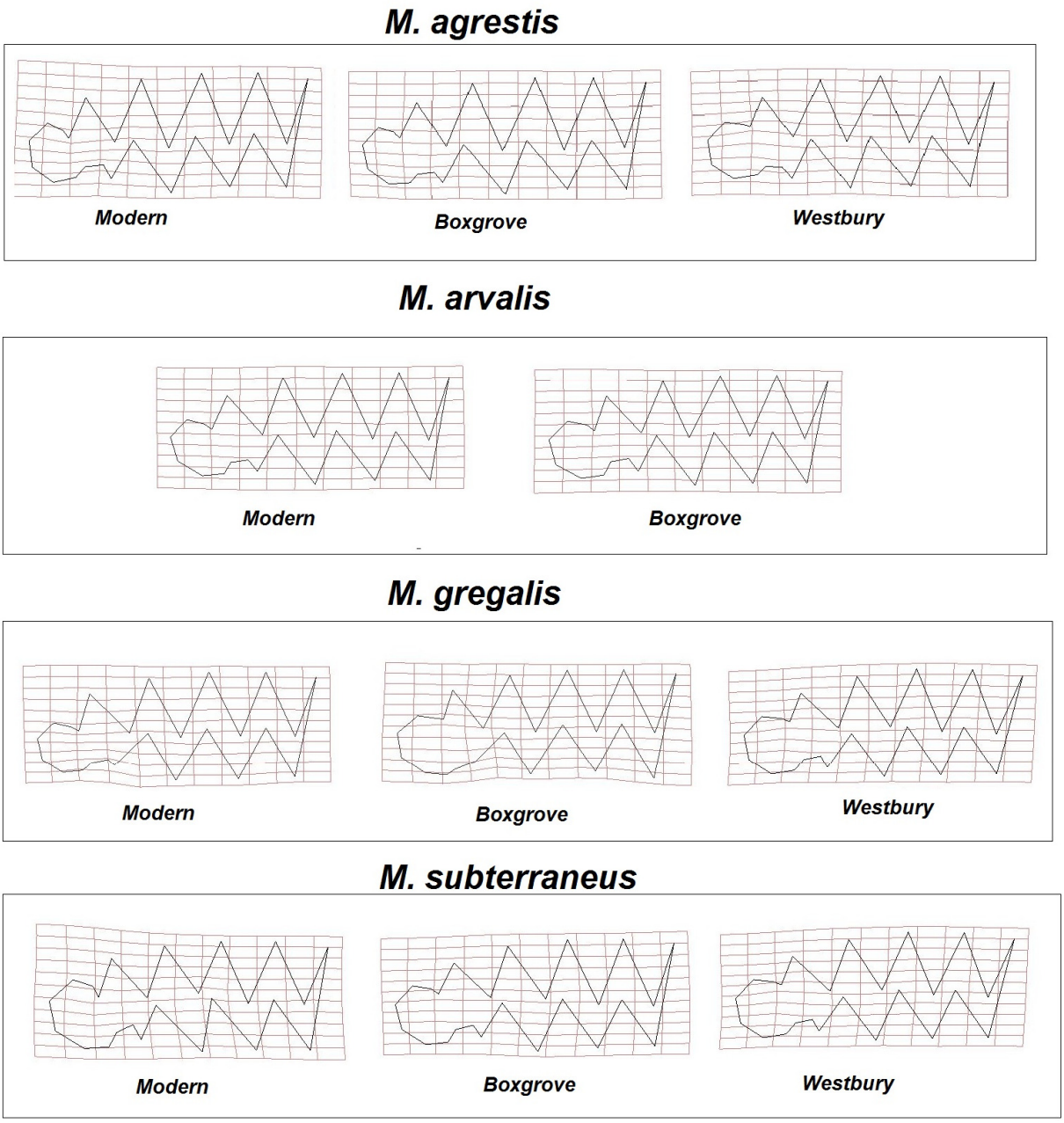

Figure 9.4: Mean shapes of each species from Modern, Boxgrove and Westbury datasets. Shapes are calculated as Cartesian transformation grids of thin plate splines against the mean shape of the species from all samples.

9.3.2: HYPOTHESIS 9.2 THERE IS NO SIGNIFICANT DIFFERENCE IN M_1 SIZE BETWEEN MODERN AND EARLY MIDDLE PLEISTOCENE *MICROTUS* OF THE SAME SPECIES.

In order to assess size differences between archaeological and modern samples of the same species, a Student's t-test is performed on the sample centroid sizes, as calculated during Procrustes fitting. Tables 9.6- 9.8 show a significant difference in size between modern and Westbury samples across all 3 species. At Boxgrove, a significant difference in size can be seen between *M. agrestis* and *M. subterraneus* from the modern sample. The insignificant result gained when the *M. gregalis* sample from Boxgrove is compared to the modern sample may be due to the small size of the Boxgrove *M. gregalis* sample (6 individuals). In all species, there is no significant difference in size between the Boxgrove and Westbury samples. In all species, the average centroid size of the modern sample is larger than that of the Boxgrove and Modern samples (Table 9.9). On the basis of the evidence presented above, hypothesis 9.2 is rejected.

	Modern	Boxgrove
Boxgrove	2.1397	
	0.0341	
Westbury	5.2649	1.6797
	0.0000	0.0942

Table 9.6: Results of a Students' T-test on M. agrestis samples, t-values are shown above associated p-values. Significant results are highlighted in yellow.

	Modern	Boxgrove
Boxgrove	0.6723	
	0.5029	
Westbury	3.9997	-0.4384
	0.0001	0.6614

Table 9.7: *Results of a Students' T-test on M. gregalis samples, t-values are shown above associated p-values. Significant results are highlighted in yellow.*

	Modern	Boxgrove
Boxgrove	3.5251	
	0.0006	
Westbury	5.0056	-0.7797
	<0.0001	0.4367

Table 9.8: *Results of a Students' T-test on M. subterraneus samples, t-values are shown above associated p-values. Significant results are highlighted in yellow.*

	M. agrestis	*M. arvalis*	*M. gregalis*	*M. subterraneus*
Modern	0.99437	0.99044	0.99209	0.993678
Boxgrove	0.99286	0.99145	0.98811	0.989805
Westbury	0.99200	-	0.98897	0.989701

Table 9.9: *Mean Centroid sizes for species from Modern, Boxgrove and Westbury samples.*

9.3.3 HYPOTHESIS 9.3: THERE IS NO DIFFERENCE IN SPECIES COMPOSITION AT BOXGROVE AND WESTBURY SUN-MENDIP.

A difference in species composition between sites is evident from the discriminant function assignment of unknown *M. arvalis*/ *agrestis* samples, as described in detail in chapter 4. Boxgrove samples are shown to contain both *M. agrestis* and *M. arvalis* specimens (appendix B). However, samples from Westbury are shown to contain *M. agrestis* only, with no *M. arvalis* specimens being identified from the entire sample of 217 individuals (appendix B). This result suggests a further difference in species

composition between the two sites. *Microtus* species present at each site are summarised in table 9.10.

	Boxgrove	Westbury
M. agrestis	*	*
M. arvalis	*	
M. gregalis	*	*
M. subterraneus	*	*
P. gregalodies		*

Table 9.10: *Summary of Microtus species present at Boxgrove and Westbury, as identified from re-substitution of samples treated as unknown during discriminant function analysis.*

In both Boxgrove and Westbury samples, all specimens displaying the *M. arvalinus* morphology (29 and 32 individuals respectively) are identified as *M. agrestis* during discriminant function analysis with re-substitution of unknown samples. All specimens are identified *as M. agrestis* both when the AC region of the tooth (the region of the tooth which varies from standard *M. arvalis/ agrestis* morphology) is included within the sample and also when only landmarks 1-15 are included, which indicates a very strong morphological similarity between *M. arvalinus* and *M. agrestis.* When cross-validation *of M. arvalinus* is performed against modern *M. arvalis, M. agrestis, and M. gregalis* and *M. subterraneus* samples, 100 percent are assigned to *M. agrestis*. Therefore, there appears to be a difference in species composition between Westbury and Boxgrove, and H 8.4 is rejected.

9.3.4 HYPOTHESIS 8.4: SAMPLES FROM BOXGROVE AND WESTBURY-SUB MENDIP HAVE NO SIGNIFICANT DIFFERENCE IN MORPHOLOGY THROUGH TIME.

There is much discussion in the literature as to the relative ages of Cromerian sites, and in particular, how close in time the Westbury and Boxgrove deposits are, with some arguing that the Calcareous member deposits at Westbury and the Boxgrove sequence have extremely similar mammalian faunas and are therefore, likely to be of approximately the same age. In order to analyse the degree of similarity between the two sites, a PCA is performed on *M. agrestis* and *M. subterraneus* datasets, each containing samples from Westbury and Boxgrove sites. No obvious groupings in the dataset are observed in PC1and PC2 or any other principal components.

Therefore, a discriminant function analysis is run on each species dataset. Table 9.11 shows the Procrustes distances between stratigraphic levels and associated p-values for *M. agrestis* and table 9.12 for *M. subterraneus*. For both species, it can be seen that the difference in morphology between the sites at most stratigraphic levels is statistically insignificant. However, in *M. agrestis* the significant results show a difference in morphology between Westbury units 11 and 15-2 and 4c at Boxgrove. *M. subterraneus* displayed a significant difference between unit 15/2 at Westbury and 4c at Boxgrove. This result does not appear to be an artefact of sample size as there is no large discrepancy between sample sizes. The difference in morphology between unit 4c at Boxgrove and units 11 and 15/2 at Westbury does not appear to be as a result of climatic conditions as all units are deposited during temperate conditions (Parfitt, 1999; Currant, 1999).

When the Procrustes distances between each stratigraphic group are illustrated using a UPGMA tree, both *M. agrestis* (Figure 9.5) and *M. subterraneus* (Figure 9.6), display a

similar pattern. In both species, all Westbury stratigraphic levels form a distinct group from the Boxgrove samples. Within the Westbury group, there is also, broadly, a separation between the unit 15 sub-units and those from the rest of the sequence, that is consistent with the pattern observed when the Westbury sample is analysed in isolation (see chapter 6 for details). On the basis of the evidence presented above, Boxgrove and Westbury samples are shown to have a significant difference in morphology between some stratigraphic levels and H2 is rejected

		WESTBURY												BOXGROVE				
		10	11	12	13	14	15-1	15-2	15-4	15-5	40770	19-13	19-14	3	4b	4c	5a	5b
WESTBURY	11	**0.031**																
		0.546																
	12	**0.028**	**0.018**															
		0.942	*0.807*															
	13	**0.025**	**0.013**	**0.023**														
		1	*0.927*	*0.669*														
	14	**0.088**	**0.026**	**0.019**	**0.023**													
		1	*0.98*	*0.661*	*0.952*													
	15-1	**0.033**	**0.023**	**0.833**	**0.024**	**0.037**												
		0.998	*0.756*	*0.823*	*1*	*0.995*												
	15-2	**0.043**	**0.025**	**0.045**	**0.027**	**0.041**	**0.018**											
		0.95	*0.095*	*0.048*	*0.58*	*0.536*	*0.788*											
	15-4	**0.044**	**0.027**	**0.056**	**0.028**	**0.041**	**0.018**	**0.086**										
		0.99	*0.093*	*0.641*	*0.995*	*0.976*	*1*	*0.438*										
	15-5	**0.046**	**0.032**	**0.036**	**0.038**	**0.043**	**0.031**	**0.034**	**0.032**									
		0.958	*0.693*	*0.997*	*0.971*	*0.965*	*0.995*	*0.955*	*0.997*									
	15-8	**0.033**	**0.034**	**0.024**	**0.031**	**0.035**	**0.055**	**0.039**	**0.039**	**0.034**								
		0.95	*0.897*	*0.779*	*0.973*	*0.563*	*0.581*	*0.027*	*0.957*	*0.945*								
	19-13	**0.041**	**0.035**	**0.029**	**0.025**	**0.038**	**0.022**	**0.022**	**0.024**	**0.033**	**0.033**							
		0.956	*0.78*	*0.961*	*0.869*	*0.99*	*1*	*0.895*	*0.999*	*0.995*	*0.951*							
	19-14	**0.037**	**0.036**	**0.028**	**0.026**	**0.031**	**0.034**	**0.037**	**0.036**	**0.033**	**0.085**	**0.032**						
		0.947	*0.039*	*0.555*	*0.038*	*0.654*	*0.921*	*0.45*	*0.85*	*0.995*	*0.972*	*0.997*						
BOXGROVE	3	**0.044**	**0.043**	**0.041**	**0.04**	**0.044**	**0.048**	**0.047**	**0.05**	**0.051**	**0.038**	**0.043**	**0.044**					
		0.984	*0.847*	*0.979*	*0.999*	*0.999*	*0.999*	*0.972*	*0.999*	*0.999*	*0.999*	*1*	*0.994*					
	4b	**0.048**	**0.045**	**0.039**	**0.043**	**0.037**	**0.052**	**0.057**	**0.059**	**0.054**	**0.041**	**0.052**	**0.044**	**0.045**				
		0.982	*0.653*	*0.897*	*0.999*	*0.986*	*0.999*	*0.935*	*0.997*	*0.991*	*0.994*	*0.993*	*0.998*	*0.952*				
	4c	**0.036**	**0.03**	**0.033**	**0.026**	**0.035**	**0.031**	**0.032**	**0.037**	**0.045**	**0.037**	**0.036**	**0.039**	**0.036**	**0.036**			
		0.691	*<0.001*	*0.943*	*0.636*	*0.702*	*0.425*	*0.99*	*0.483*	*0.702*	*0.383*	*0.769*	*0.497*	*0.988*	*0.985*			
	5a	**0.046**	**0.036**	**0.042**	**0.032**	**0.046**	**0.03**	**0.03**	**0.037**	**0.044**	**0.038**	**0.034**	**0.038**	**0.039**	**0.045**	**0.032**		
		0.963	*0.583*	*0.915*	*0.965*	*0.957*	*0.961*	*0.585*	*0.977*	*0.961*	*0.956*	*0.983*	*0.98*	*0.996*	*0.986*	*1*		
	5b	**0.045**	**0.045**	**0.048**	**0.043**	**0.052**	**0.042**	**0.04**	**0.043**	**0.056**	**0.045**	**0.041**	**0.049**	**0.032**	**0.058**	**0.039**	**0.037**	
		0.981	*0.624*	*0.901*	*0.992*	*0.852*	*0.991*	*0.699*	*0.998*	*0.901*	*0.979*	*0.971*	*0.87*	*0.999*	*0.058*	*0.689*	*0.972*	
	6	**0.033**	**0.034**	**0.03**	**0.028**	**0.031**	**0.039**	**0.041**	**0.046**	**0.047**	**0.029**	**0.038**	**0.034**	**0.031**	**0.03**	**0.022**	**0.03**	**0.041**
		0.968	*0.496*	*0.876*	*0.995*	*0.992*	*0.978*	*0.825*	*0.919*	*0.958*	*0.982*	*0.038*	*0.954*	*1*	*0.999*	*0.969*	*0.996*	*0.997*

Table 9.11: Results of a discriminant function analysis of M. agrestis by stratigraphic level at Westbury and Boxgrove. Procrustes distances are shown in bold and associated p-values in italics.

		Westbury								Boxgrove					
		10	12	13	14	15-1	15-2	15-4	15-5	3	4b	4c	5a	5b	6
Westbury	12	**0.042**													
		0.989													
	13	**0.039**	**0.043**												
		0.987	*0.995*												
	14	**0.025**	**0.035**	**0.032**											
		1	*0.996*	*0.997*											
	15-1	**0.051**	**0.035**	**0.057**	**0.046**										
		0.917	*0.989*	*0.96*	*0.877*										
	15-2	**0.052**	**0.031**	**0.057**	**0.045**	**0.019**									
		0.781	*0.92*	*0.676*	*0.312*	*0.581*									
	15-4	**0.051**	**0.037**	**0.055**	**0.044**	**0.022**	**0.015**								
		0.911	*0.973*	*0.909*	*0.895*	*0.91*	*0.616*								
	15-5	**0.049**	**0.037**	**0.056**	**0.046**	**0.021**	**0.023**	**0.021**							
		0.972	*0.939*	*0.935*	*0.915*	*0.91*	*0.694*	*0.984*							
Boxgrove	3	**0.049**	**0.043**	**0.059**	**0.042**	**0.036**	**0.032**	**0.031**	**0.04**						
		0.959	*0.999*	*0.976*	*0.983*	*0.988*	*0.902*	*0.994*	*0.99*						
	4b	**0.052**	**0.049**	**0.052**	**0.046**	**0.041**	**0.038**	**0.035**	**0.038**	**0.037**					
		0.916	*0.991*	*0.984*	*0.956*	*0.996*	*0.833*	*0.996*	*0.993*	*0.943*					
	4c	**0.048**	**0.046**	**0.053**	**0.044**	**0.033**	**0.034**	**0.03**	**0.036**	**0.028**	**0.027**				
		0.93	*0.816*	*0.805*	*0.918*	*0.494*	*<.0001*	*0.087*	*0.829*	*1*	*0.998*				
	5a	**0.058**	**0.053**	**0.063**	**0.053**	**0.036**	**0.037**	**0.032**	**0.038**	**0.027**	**0.032**	**0.025**			
		0.943	*0.976*	*0.803*	*0.932*	*0.989*	*0.645*	*0.961*	*0.99*	*0.995*	*0.992*	*0.973*			
	5b	**0.061**	**0.058**	**0.071**	**0.055**	**0.05**	**0.049**	**0.046**	**0.053**	**0.038**	**0.046**	**0.04**	**0.043**		
		0.993	*0.989*	*0.875*	*0.993*	*0.996*	*0.794*	*0.995*	*0.995*	*0.994*	*0.953*	*0.981*	*0.99*		

Table 9.12 : *Results of Discriminant Function analysis of M. subterraneus by stratigraphic level at Boxgrove and Westbury. Procrustes distances are shown in bold and associated p-values in italics..*

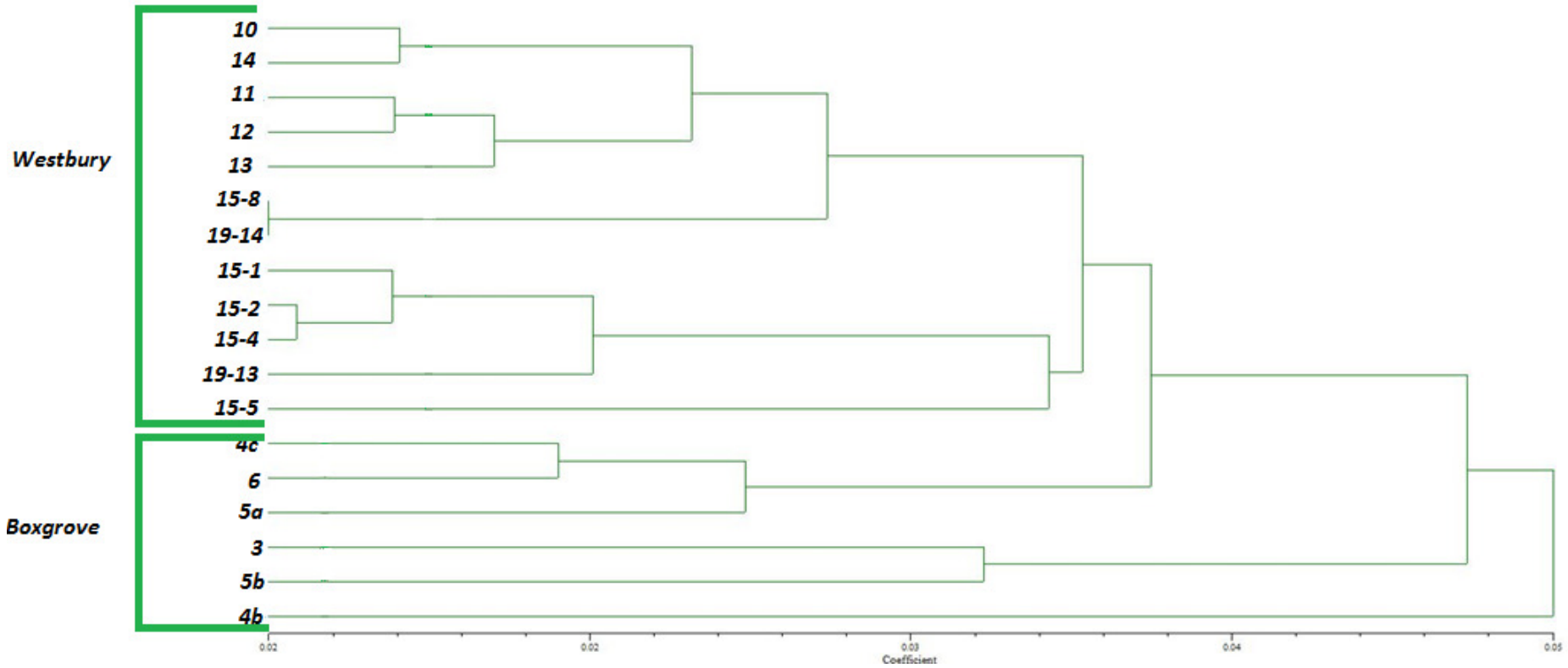

Figure 9.5: *UPGMA tree illustrating Procrustes distances between M. agrestis samples from Westbury and Boxgrove.*

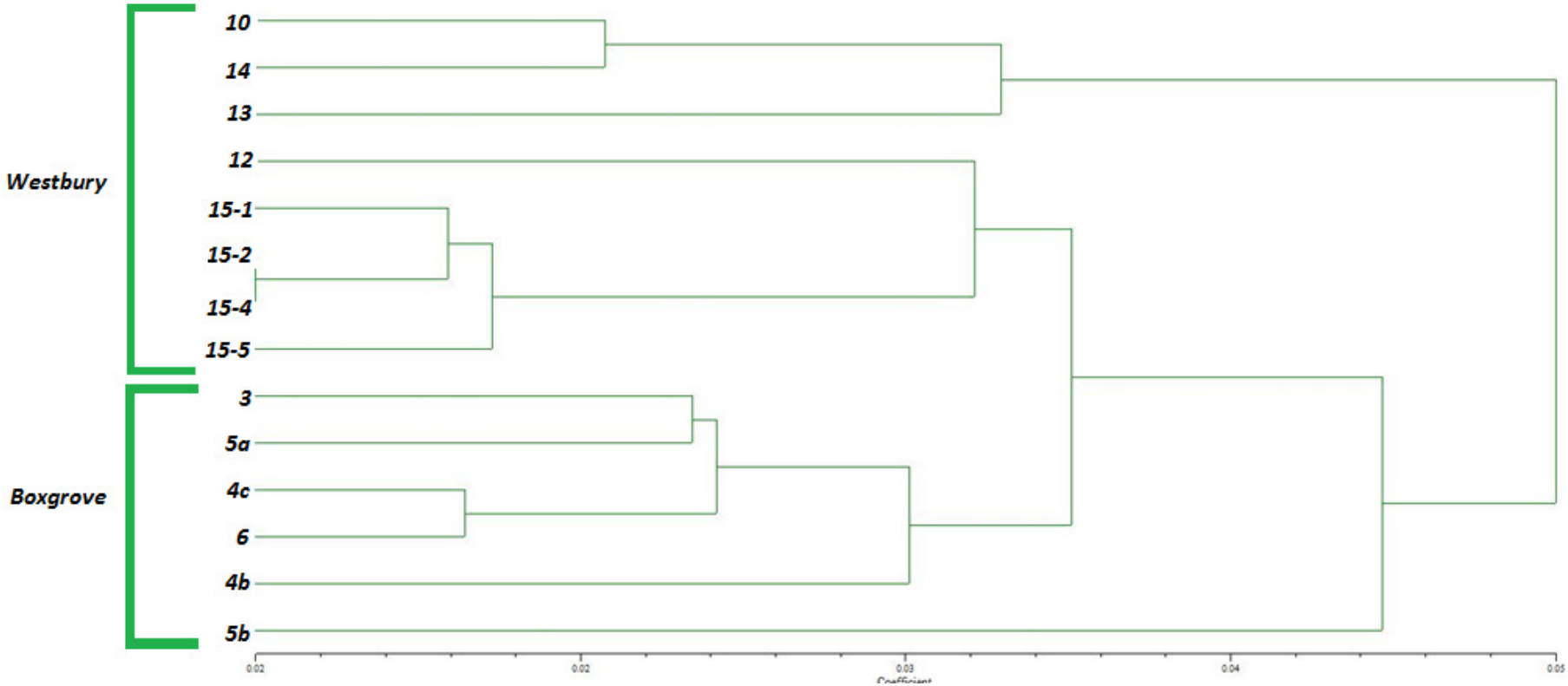

Figure 9.6: *UPGMA tree illustrating Procrustes distances between M. subterraneus samples from Westbury and Boxgrove*

9.3.5 HYPOTHESIS 9. 5: SPECIMENS FROM BOXGROVE AND WESTBURY WILL HAVE NO SIGNIFICANT DIFFERENCE IN MORPHOLOGY TO THOSE FROM THE MIDDLE PLEISTOCENE SITES AT CUDMORE GROVE AND WEST RUNTON.

Westbury and Boxgrove contain the largest well-preserved, well stratified mammalian deposits from the Early Middle Pleistocene in Britain. Other sites from the Early Middle Pleistocene have very small numbers of intact *Microtus* molars, and therefore, the number of sites available for comparison to the Westbury and Boxgrove samples is limited to Cudmore Grove, a post-Cromerian, late Middle Pleistocene (MIS9) site and West Runton, dated to MIS 19-17. *M. arvalis* remains have been recovered in relatively large numbers from both sites and are included in the following analyses.

Firstly, a PCA is performed upon Procrustes-fitted coordinates to summarise the major axis of variation within the sample. No clear separation of samples from each site could be determined on PC1 and PC2 or any other axis. Therefore, in order to investigate the relationship between datasets, a discriminant function is performed. Results are shown in Table 9.13. The results of the discriminant function analysis show samples from all locations to be statistically significantly different from one another. Cross-validation results show that at least 98 percent of specimens can be correctly identified in all cases (table 9.15).

When the relationship between Procrustes distances is plotted as a UPGMA tree, it could be seen that Boxgrove and Westbury samples are more similar to one another than they are to either West Runton or Cudmore Grove (Figure 9.5). The West Runton sample is shown to be the most morphologically distinct.

Therefore, hypothesis 9.5 is rejected.

	Boxgrove	Cudmore	Westbury	West Runton
Cudmore	**0.025704**			
	<.0001			
Westbury	**0.025666**	**0.028845**		
	<.0001	<.0001		
West Runton	**0.033491**	**0.038508**	**0.032836**	-
	<.0001	<0.0001	<.0001	-

Table 9.13: *Results of Discriminant Function analysis of M. subterraneus between Boxgrove, Cudmore Grove, Westbury and West Runton. Procrustes distances are shown in bold and associated p-values in italics.*

	Boxgrove	Cudmore	Westbury	West Runton
Boxgrove	98	0	2	0
Cudmore	0	100	0	0
Westbury	1	0	99	0
West Runton	0	0	0	100

Table 9.14*: Results of a cross-validation analysis of M. subterraneus from Boxgrove, Cudmore Grove, Westbury and West Runton. Values are shown as proportion of samples from a sample assigned to each sample.*

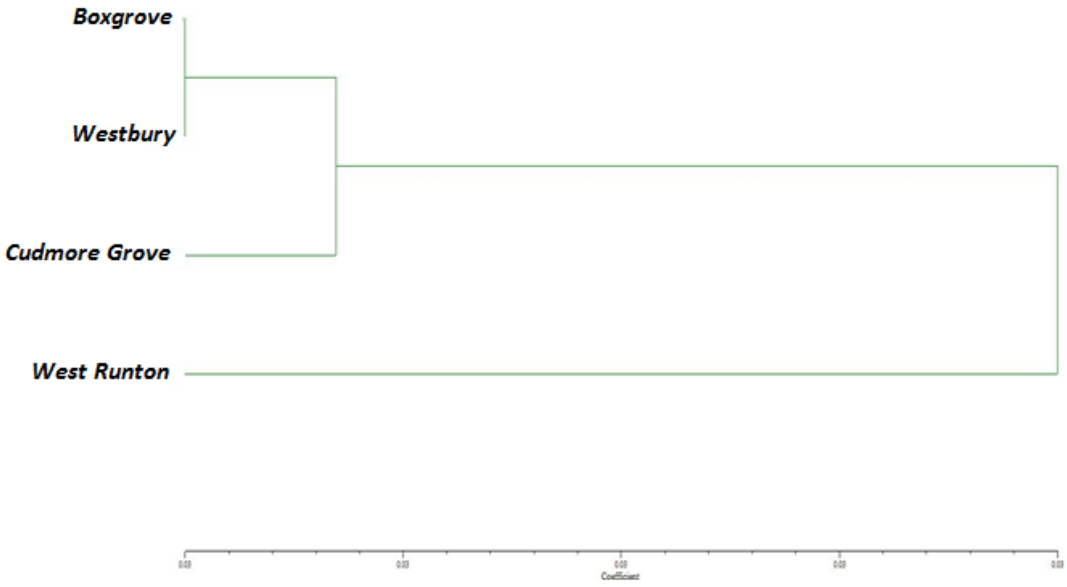

Figure 9.7: *UPGMA tree illustrating Procrustes distances between M. agrestis samples from sites of Middle Pleistocene age.*

9. 4 DISCUSSION

The preceding analyses and results have provided evidence for the degree of separation between specimens from modern and archaeological contexts, as well as evaluating the current taxonomic position of archaeological samples. The analyses have also attempted to investigate the chronological position of the Boxgrove and Westbury sub-Mendip sites, in relation to one another and to other Cromerian sites within Britain.

These analyses provide an opportunity to evaluate the potential of GMM methods in the correlation of *Microtus*-bearing sediments between sites.

When comparing morphology within a species between archaeological and modern datasets, it has been demonstrated that there is a highly significant difference in morphology between the early Middle Pleistocene specimens from Westbury and

Boxgrove, and those collected from a geographically diverse range of modern locations. This is largely unsurprising, as *Microtus* species are known to have evolved extremely rapidly (as discussed elsewhere in this study). Given the results presented within H 8.1, rapid morphological and genetic evolution in the *Microtus* species included within this study is supported over the c. 500,000 year period between the Early Middle Pleistocene and the present day. During this time, there have been several extinctions and re-introductions of *Microtus* species within the British Isles and throughout Europe. Ranges of *Microtus* species have expanded and contracted over time, leading to dispersal of populations and gene-flow between different populations.

In *M. arvalis* and *M. agrestis*, Westbury and Boxgrove samples are shown to be morphologically more similar to each other than to their modern counterparts. *P. gregalodies* samples from Westbury are shown to be morphologically very distinct from the *M. gregalis* samples from Boxgrove and modern samples. Given that *P. gregalodies* displays a 'Pitymoid' morphology, which has been suggested as a morphological stage through that all *Microtus* species evolved, this supports the suggestion that *P. gregalodies* is ancestral to *M. gregalis,* and therefore, that the sediments at Westbury are likely to pre-date those at Boxgrove.

The large separation shown between modern *M. subterraneus* specimens and all other samples suggest there is a major biological difference between modern and archaeological *M. subterraneus*. As archaeological *Microtus* remains are commonly subjected to taphonomic factors resulting in heavy modification and breakage of skeletal elements (i.e.; digestion by birds of prey, breakage due to sediment movement etc), the sole method of species identification is usually based upon the M_1, with other skeletal elements that are used by taxonomists in modern specimens, such as skull

dimensions being unavailable. Therefore, it is possible that specimens identified as *M. subterraneus* in archaeological and palaeontological contexts on the basis of their M_1 morphology belong to another (possibly extinct) species that shared a common M_1 morphology with modern-day *M. subterraneus*.

In all species, samples from Boxgrove display a reduced variance when compared with Modern and Westbury samples. The cause of this reduced variance is likely to be twofold; Firstly, as can be seen in chapter 7, the rapidly deposited Boxgrove sample is extremely homogeneous. As the site at Boxgrove is thought to represent a relatively short time-span in comparison with the Westbury Cave sediments, the opportunity for identifiable morphological changes as a result of evolutionary, biological or ecological factors to have occurred is much reduced. Secondly, as *Microtus* species are known to have a high degree of inter-populational variation (Gutherie, 1966, Jaarola et al., 2004), it would be expected that a sample from a single geographic location would have a reduced variance in comparison with the modern sample, which includes individuals from several geographically diverse populations,

Ancient samples are identified to species level based upon their similarity to extant species. This leads to the possibility of mis-identifying archaeological samples that have a divergent genetic lineage to modern specimens but share morphological characteristics. In the case of archaeological *M. subterraneus*, the species became extinct within the British Isles before or during the early stages of MIS 11, approximately 400, 000 years ago (Schreve, 2001). Due to the age of these samples, DNA analysis is not possible, and therefore, the only criteria for identification are morphological characteristics, which can be problematic, as discussed above. It is also possible that modern *M. subterraneus* is derived from a small founder population, due

to an extinction event leading to a genetic bottle neck in surviving populations. Alternatively, it is possible that at some point between the early Middle Pleistocene and the present day, an event, such as a dramatic reduction of populations caused by climatic changes, has occurred that has caused a genetic bottle-neck within *M. subterraneus*, increasing genetic drift and leading to the emergence of differing morphologies and/ or speciation to occur. As all other modern species within this study are significantly closer to their palaeontological counterpart than to any other species, it appears unlikely that the extremely large divergence between modern and Early Middle Pleistocene M. subterraneus samples is an artefact of the increased geographical range of the modern samples.

It has been demonstrated that, in addition to there being a morphological difference between modern and archaeological datasets within this chapter, there are also significant size differences. In all species, the modern samples are shown to be slightly larger than their archaeological counterparts. Additionally, no statistically significant difference in size is observed between Westbury and Boxgrove samples in any species. This difference in size between archaeological and modern is consistent throughout all stratigraphic levels (archaeological) and geographic locations (modern) when compared individually. Therefore, difference in size between samples does not appear to have been an artefact of the large geographic source of the modern samples or the large period of time covered by the archaeological samples.

The mechanism by which modern *Microtus* dentition has increased in size in comparison with ancient specimens is not clear. The uniformity of tooth size across all stratigraphic levels in archaeological material and all geographic locations in modern material would suggest that tooth size is not solely influenced by climatic change, as

has been discussed in chapters 5-8 .Assuming that an increase in tooth size is indicative of an increase in body size, an increase in body size over time is in agreement with Cope's rule that population lineages tend to increase in body size over evolutionary time as increased body size enhances an organism's ability to avoid predators, improves thermal efficiency and increases successful reproduction (Hone & Benton, 2005). It has also been suggested that an evolutionary increase in size over time may represent a trend towards the optimal body size of a species (Alroy, 1998).

Specimens displaying the '*M. arvalinus'* morphotype are found within the *M. arvalis/ agrestis* samples at Westbury, Boxgrove and West Runton. This palaeontological 'species' was originally identified by Hinton (1923) and has been assumed to be a morphology found in ancient specimens of *M. arvalis*. Many authors have identified the presence of this distinct morphology within early Middle Pleistocene samples (see chapter 3 for further details). Chaline (1972) has suggested that the *M. arvalinus* morphotype is a synonym of *M. arvalis*, whereas Sutcliffe & Kowalski (1975) argued that there is no evidence to suggest the selection *of M. arvalis* as a synonym rather than *M. agrestis*. Discriminant function analysis of modern *M. arvalis* and *M. agrestis* specimens has shown it is possible to separate the specimens using a discriminant function analysis with one hundred percent accuracy (Chapter 5). Using this discriminant function analysis, *M. arvalinus* specimens from both Boxgrove and Westbury are shown to be morphologically more similar to modern *M. agrestis* samples, with all *M. arvalinus* specimens being assigned to this species. This result is consistent both when the AC region of the tooth is included in the analyses and when only the triangular portions of the tooth are included, suggesting the morphological affinity with *M. agrestis* is extremely strong. These results suggest that, with further

investigation, the traditional taxonomic position of *M. arvalinus* may need to be revised. As *M. arvalis* and *M. agrestis* share similar, wide ranging habitat preferences, and frequently co-exist in the modern day this finding does not affect the palaeoecological interpretation of these sites. However, there is potential of these techniques to contribute to palaeoclimatic interpretations through correctly identifying relationships between morphotypes in other material. This finding also suggests that application of GMM methods to *Microtus* teeth may be of use in determining evolutionary relationships in specimens which display a similar (but distinct) morphology to modern specimens and have been assumed to be part of that evolutionary lineage.

Evidence from the discriminant function analysis of *M. arvalis/ agrestis* specimens at Westbury shows that, when compared with modern *M. arvalis/ M. agrestis*, all Westbury specimens are assigned to *M. agrestis*. The presence of *M. agrestis* at the site had been suggested by the presence of the characteristic M^2 teeth within some samples, however, it had previously been suggested that the sample contained individuals of both *M. arvalis* and *M. agrestis*, although no indication has been given in the published literature of any evidence of *M. arvalis* M^2 remains being found at the site. (Currant, 1999. Andrews, 1990). This is in contrast to Boxgrove, where a mix of *M. arvalis* and *M. agrestis* is found, both within the published literature and within this study. The biostratigraphic significance of the presence of *M. arvalis* and *M. agrestis* within the Cromerian has not been investigated due to the previous difficulty in separating dental remains of the two species, however, these results suggest that the relative presence and absence of these species could provide significant insight into the chronological relationships between sites.

The large number of specimens recovered from Westbury and included within this study (see table 8.1 for details) makes it improbable that the species-bias is an artefact of sampling. Both *M. arvalis* and *M. agrestis* have similar climatic and habitat tolerances (Gromov & Polyakov, 1992) and are able to exist successfully within the range of habitats found at Westbury, suggesting that the absence of *M. arvalis* is not caused by habitat or climatic differences. Additionally, both species are predated on by similar predators (Andrews, 1990), so it is unlikely that differences in predator accumulation of the remains could be a factor. Therefore, the difference in the composition of the mammalian faunas at Westbury and Boxgrove suggests they may not represent the same period in time, despite the similarity in the composition of their mammalian faunas. This is a highly significant finding as understanding the relative chronology of sites within the British early Middle Pleistocene is key in understanding several areas including, evolution of species, the colonisation history of the British Isles and palaeoclimatic reconstructions.

In order to investigate the morphological difference between Boxgrove and Westbury populations further, discriminant function analyses are performed on the combined datasets, focusing upon the difference between stratigraphic levels in both sites. Although the samples from each site are shown to be statistically significantly different when the site datasets as a whole are observed, when individual stratigraphic units are analysed, no significant difference in morphology is found between most stratigraphic levels.

However, despite the apparent similarity between stratigraphic levels at each site, when the Procrustes distances between samples are compared using UPGMA trees constructed from Procrustes distances between samples, it can be seen that the

samples clearly cluster into two separate groups according to which site they originate from. Within each site, there are also clusters which are similar in both datasets. In both *M. agrestis* and *M. subterraneus*, both Westbury datasets are split into 2 main groups- unit 15 sub-units forming one group and all other stratigraphic levels within another that is similar to the pattern observed in chapter 7.

Although throughout the samples, the majority of stratigraphic levels are not significantly different in morphology from one another, the fact that the two sites cluster into two distinct groupings suggests that there is likely to be a difference in age between the two sites, perhaps representing different small-scale climatic fluctuations within the same interglacial cycle (MIS 13), as suggested by Parfitt and Preece (2001). It is also possible that the populations are of the same age and are very localised, with little or no genetic mixing between them therefore developing significant differences in morphology. However, when the differences in faunal composition are also taken into account, it seems more likely that the sites are of a different age.

It is important to note that, in both samples, units 15/2 and 11 are shown to be significantly different from level 4c at Boxgrove. As described in the introduction to this chapter, units 11, 15/2 and 15/4 at Westbury have been suggested to be of the same age as level 4c at Boxgrove, based upon the composition of their faunal assemblages. However, the results of hypotheses 1 and 2 suggest that the sites can be of different ages, as suggested by Parfitt & Preece (2000). These findings are supported by the literature (e.g. Preece & Parfitt, 2001) that suggests the presence of *P. gregalodies* at Westbury implies an older age for the site, as *P. gregalodies* is thought to be an ancestral form of *M. gregalis*, as found at Boxgrove (Currant. 1999), and is shown to be highly morphologically distinct from the *M. gregalis* specimens

found at Boxgrove. When the Bootstrapped variance values are analysed, it can be seen there is a reduced variance within the Boxgrove sample compared with the Westbury sample. This difference is likely to reflect the relatively short period of time represented at Boxgrove in comparison with the Westbury stratigraphic sequence, which is believed to have been deposited over a significant period of time (Andrews et al., 1999, Roberts & Parfitt, 1999).Although few *Microtus* samples recovered from British Pleistocene sites other than Westbury and Boxgrove are suitable for analysis, Westbury and Boxgrove samples are demonstrated to be more similar morphologically than those from both younger (Cudmore Grove) and older (West Runton) sites. This result correlates with the biostratigraphic model proposed for the Pleistocene in the Britain. Therefore, the results gained in this study suggest that if samples become available, it may be possible to create a relative age-model using geometric morphometric analysis of the *Microtus* $M_{1.}$ This model can be used to strengthen current biostratigraphic models and has the potential to resolve the relative position of closely-related sites.

The research presented above has several implications for further research; the potential of *Microtus* remains to discriminate between samples where the relative dating of the sites is in question has been demonstrated. This is a common occurrence within archaeological and palaeontological deposits, particularly in pre-Holocene sites where common absolute dating techniques such as radiocarbon dating are not always applicable.

The application of geometric morphometric techniques to questions of taxonomy and relatedness of archaeological and modern material has also been suggested through these results to have potential applications.

The suggestion that Westbury and Boxgrove are not of the same age, supports the evidence given by Parfitt and Preece (2000) and increases the strength of the argument that Westbury sub-Mendip pre-dates Boxgrove and that the sites are likely to belong to Cromerian interglacials III and IV respectively.

9.5 CONCLUSIONS

In light of the evidence presented above, there are several conclusions that can be drawn;

- There is evidence of significant morphological change between *Microtus* M_1 from the early Middle Pleistocene sites and modern samples. There is also a smaller, but still significant difference in morphology between the Early Middle Pleistocene sites of Westbury and Boxgrove.
- Modern *M. subterraneus* samples display an extremely large difference in morphology in comparison with all other modern and archaeological samples. The morphological distance between modern *M. subterraneus* specimens and those from Westbury and Boxgrove is larger than distances found between all other species. Therefore, it is possible that modern *M. subterraneus* have not evolved from Early Middle Pleistocene samples, or that a genetic bottleneck has occurred.
- Evidence has been found of significant differences in the *Microtus* species composition between Westbury and Boxgrove. This difference in composition supports the theory that, although these sites may belong to the same MIS, there is a significant difference in their age.

- Based upon the results of discriminant function analyses, specimens displaying the '*M. arvalodiens'* morphology are shown to be morphologically most similar to *M. agrestis* rather than *M.arvalis*, as had previously been suggested. Therefore, a taxonomic revision of this morphotype is suggested.
- Specimens from different stratigraphic levels at Westbury and Boxgrove are shown to be similar in morphology when compared to one another. However, the overall site samples remain significantly different.
- It is proposed that it may be possible to use the morphology of *Microtus* M_1 teeth to identify the chronological relationship between sites.

CHAPTER 10
SUMMARY AND CONCLUSIONS

10.1 SUMMARY OF RESULTS AND CONCLUSIONS OF THE STUDY.

The aim of this study has been threefold; firstly to evaluate the application of Geometric Morphometric methods to *Microtus* M_1 teeth; secondly, to investigate variation in the form of *Microtus* M_1 in modern material and thirdly, to investigate variation in M_1 morphology in the Early Middle Pleistocene, and to investigate factors which affect this variance. The genus *Microtus* is known to be one of the most rapidly evolving species throughout the Quaternary period (Gutherie, 1964), and have been shown to demonstrated a high degree of inter and intra-specific genetic variability (Jaarola, 2004; Jaarola & Searle, 2002; Jaarola & Searle, 2004)

The teeth of Microtine rodents are one of the skeletal elements most resistant to taphonomic interference and breakage (Andrews, 1990). Therefore, M_1 remains of *Microtus* are often extremely common in Pleistocene sediments throughout Europe. Previous research using standard morphometric techniques has suggested that *Microtus* teeth may be used as a proxy for both phylogeographic relationships and climatic conditions (e.g. Krystufek & Vohralik, 2004; McGuire, 2009, Polly, 2003, Mointure & Brunet-Lecomte, 2004).

Geometric Morphometric techniques have been extensively used to investigate many morphological factors of biological interest, such as allometry, asymmetry, taxonomy

and phylogenies. GMM methods have shown great advantages over standard metric techniques when used to analyse biological material, and were therefore selected for this project.

Therefore, with the expectation of the ability to identify and investigate rapidly evolving changes in M_1 morphology in both modern and archaeological populations using GMM techniques, this study examines morphological variation both within and between populations of *M. agrestis*, *M. arvalis*, *M. gregalis* and *M. subterraneus* and their extinct counterparts, *M. arvalodiens*, P. arvalodies and *P. gregalodies*. The results of each of the major aims of the study, as erected in chapter 1 will be summarised in turn and conclusions drawn below.

To use modern species to create species identification criteria based on the geometric morphometric protocol.

Inter-specific variation in *Microtus* species has been studied for several centuries and there are well-defined standard classification criteria for various biological characteristics, including M_1 morphology, as outlined in chapter 3. Throughout all *Microtus* species, the region of the M_1 that is considered to be the most variable and therefore, the most useful in discriminating between species is the anterior section of the tooth, a complex curved structure known as the anteroconid complex (Van der Meulen, 1973; Gutherie, 1964). Despite the large degree of intra-specific and intra-population variation, many modern species have clearly distinct M_1 morphology, and therefore are readily identified using standard, qualitative methods. Of the modern species included within this study, M_1 teeth of *M. gregalis* and *M. subterraneus* are easily distinguished on the basis of the distinctive morphology of the anteroconid

complex. By comparison, the M_1 morphology of *M. arvalis* and *M. agrestis* is too similar to be separated qualitatively. Quantitative methods of separation using the relative length of the anteroconid complex have been suggested by Nadachowski (1984) and Fedyk & Ruprecht (1971). However, these methods fail to account for relative size differences between populations, and are therefore limited in their application. As demonstrated in chapter 5, the Geometric Morphometric methodology proposed for this study is able to distinguish between all species of *Microtus* within this study with one hundred percent accuracy.

Additionally, when the AC region of the tooth is removed from analyses, the ability to distinguish between species is not reduced. This result is of considerable importance, as previous studies have assumed that the AC region of the M_1 is the only region containing significant morphological variation which could be used for taxonomic purposes (Fedyk & Ruprecht (1971), Chaline, 1972, Gutherie, 1964) this result is also of importance in archaeological assemblages where taphonomic processes frequently lead to the teeth becoming damaged. The AC region of the M_1 is the most frequently damaged part of the tooth (Andrews, 1990), but the results of these analyses show that it is possible to identify M_1 teeth to species level with a high degree of accuracy when the AC region is excluded. Therefore, it is concluded that it is possible to separate all species of *Microtus* within this study using GMM analysis and that all regions of *Microtus* M_1 teeth contain strong taxonomic signals. In conclusion, both landmark methodologies included within this study provide excellent identification criteria for modern *Microtus* species and would be expected to perform well if applied to other *Microtus* species. Using GMM methods to identify these specific species of *Microtus* represents new research, as does the finding that GMM methods can

successfully be used to identify species when the AC region of the tooth is excluded or missing.

To quantify the range of morphological variation within both fossil and modern populations, as well as the amount of geographical variation that is present between populations.

This study investigates several aspects of morphological variation in fossil and modern populations of *Microtus* and provides qualitative descriptions of the amount of morphological variance within and between populations.

M_1 samples taken from modern datasets are shown to have a larger amount of static allometry in the M_1 than that found in archaeological populations. However, throughout all samples, the amount of allometry observed is relatively low (< 10 percent of the overall variation within the sample could be attributed to the effect of size on shape), with the exception of modern *M. gregalis* samples, which displayed approximately 20 percent of the total variance within the dataset being attributed to allometry.

Analyses of modern samples show that there is no discernable sexual dimorphism in the teeth of *Microtus* species, and the same can be assumed to be true of archaeological samples.

It is been demonstrated within chapter 1 that there is a strong genetic component to variability within *Microtus* teeth, which produces similar distances between samples to those produced from analysis of *Microtus* DNA. Both genetic relationships between species and phylogeographic relationships within species are relatively well matched

to tree diagrams produces showing the relationship of morphological distances between species.

The identification of taxonomic revisions to Microtus where appropriate.

It has previously been suggested that Early Middle Pleistocene specimens displaying the *M. arvalinus* morphology (Hinton, 1923) are an ancestral form of *M. arvalis* (e.g. Chaline 1972, Hinton, 1923). Sutcliffe and Kowalski (1976) suggested that although this specific morphology is occasionally found within modern *M. arvalis* samples, there is no direct evidence to support *M. arvalinus* being an ancestral species to *M. arvalis* rather than *M. agrestis*, which displays an extremely similar M_1 morphology. It is found in Chapter 9 that all specimens from Westbury and Boxgrove displaying this morphology are found to be more similar morphologically to *M. agrestis* than to *M. arvalis*. The association between M. arvalinus and *M. agrestis* is extremely strong, with all specimens being assigned to *M. agrestis* both within the discriminant function and also upon cross-validation. Although the AC region of the tooth is the morphological feature on which M. arvalinus is identified, when this region of the tooth is excluded from analysis, leaving only T1-T5, all M. arvalinus specimens remain their affinity with modern *M. agrestis*, with no specimens being assigned to *M. arvalis* during discriminant function analysis or cross-validation. On the basis of the evidence that morphological similarity between the M. arvalinus and *M. agrestis* is extremely strong, it is therefore proposed that a taxonomic revision of M. arvalinus to an archaic form of *M. agrestis* is strongly indicated.

These analyses also discovered an extremely large difference in morphology between modern and early Middle Pleistocene *M. subterraneus*. The divergence is so large that the morphological distance between what are assumed to be archaic and modern examples of the same species are, in fact, larger than that seen between all other species. Such a large divergence in morphology is atypical when compared with the other species within this study and may have several causes; firstly, it may be as a result of an extreme genetic bottle neck between the early Middle Pleistocene and the present day. Secondly, it may be that specimens identified as *M. subterraneus* are, in fact, an entirely separate species which happens to display convergent evolution and display the same morphological features as one another.

In all other specimens, modern and Early Middle Pleistocene examples of the same species are shown to be more similar morphologically to one another than they are to another species. This suggests they represent part of the same genetic lineage and therefore, not taxonomic revision of *M. arvalis*, *M. agrestis* or *M. gregalis* is indicated.

Use of data gained from this study to allow the revision of current and development of new- biostratigraphic models using Microtine rodents for the dating of European Palaeolithic sites- particularly revision and correlation of the stratigraphic sequences at two important British Early Middle Pleistocene sites, Westbury-sub-Mendip and Boxgrove.

This study attempts to use GMM analysis of Early Middle Pleistocene *Microtus* remains and apply them to biostratigraphic questions. The relative ages of Westbury and Boxgrove have been debated, with some authors suggesting that the similarity in the

composition of their faunal assemblages indicates that they are of approximately the same age (Andrews & Stringer, 1999; Schreve et al., 1999) whereas other authors have suggested that Westbury sub-Mendip is older (Parfitt & Preece, 2001). It was proposed in the introduction to this study that the rapid rate of evolution of *Microtus* species and the high level of inter- and intra-population variance should allow morphological change within and between stratigraphic levels to be identified and used in relative dating.

Comparative analyses of morphological and size differences within each site had variable results. No significant difference between stratigraphic levels is observed in either the Walou Cave or Boxgrove samples. In the case of Boxgrove, it is likely that the relatively short deposition time represented by the stratigraphic sequence means there was a limited opportunity for distinctive morphological traits to evolve. The reason for the lack of differentiation between stratigraphic levels at Walou cave, a sequence that covers circa 100, 000 years, is less clear, as this is a significant amount of time for some morphological variation to have evolved. It is however possible that the small available sample sizes from this site led to the inability of statistical techniques to identify and differentiate between any morphological differences which did occur. In contrast to the Walou and Boxgrove samples, there are significant differences between many of the major stratigraphic levels, with sub-units from the same level showing no significant difference in most cases. This morphological disparity between levels does not appear to be a result of climatic changes, and, therefore must be as a result of evolutionary, genetic or other environmental factors.

Analyses of variance in morphology between Westbury and Boxgrove show a clear difference between each of the sites when the samples are analysed as a whole.

However, when each stratigraphic level is analysed separately, no significant difference in Morphology is observed between most levels. The reason for clear morphological difference between the sites on a large scale, but not on a small scale is not clear. It may again, be an artefact of the relatively small sample sizes available at Boxgrove. However, it also raises the possibility that what is being observed is a result of geographical variation between samples of the same age rather than between samples of differing ages.

When both Westbury and Boxgrove samples are compared with those of a much younger and a much older site MIS 9 Cudmore Grove (Schreve, 2001) and MIS 17-19 West Runton (Stuart and Lister, 2001) a significant difference between all sites is observed. While it may be true that this difference represents evolutionary changes in M_1 morphology over time, this cannot be confirmed without further investigation to gain a clear understanding of the degree of geographic variation between populations.

In conclusion, these results do not provide a clear picture as to the accuracy of applying GMM techniques to biostratigraphic questions. *Microtus* species display a large degree of phenotypic variability, which means it is difficult to show stratigraphic trends or patterns across stratigraphic levels. No clear morphological trend is identified at any of the sites, relating either to evolutionary or genetic changes due to migrations and population change. Thus, the results of this study question the validity of attempting to use GMM methods to answer biostratigraphic questions in a species such as *Microtus* which displays such a large degree of phenotypic variability, beyond the commonly used methods of biozonation boundaries (first appearance datum and last appearance datum).

Use of the Microtine assemblages to evaluate climatic changes at Westbury and Boxgrove and the effect of palaeoenvironmental change on Microtus morphology.

This study shows that climatic conditions have a significant effect upon the variance in both the size and shape of *Microtus* M_1 teeth.

When all samples from stratigraphic levels at Westbury Cave with similar climatic reconstructions (c.f. Andrews, 1999) are combined and analysed for differences in size between groups, results of a Students' t-test show that, for all species, a statistically significant difference in size between cold and temperate groups is found, with samples from cooler conditions being larger than those from warmer conditions. The finding is in agreement with Bergmann's rule, which states that species living in cold conditions will become larger as a mechanism to conserve heat loss (Bergman, 1847). However, it is in disagreement with studies published by Nadachowski (1984) and Mointure and Brunet-Lecomte (2004), who found that in *Microtus nivalis* and *Microtus grafi* respectively, the opposite relationship is found, with tooth size increasing slightly in warmer conditions. However, in both studies, no strong correlation between tooth size and climatic conditions is found, unlike in this study, where results are highly statistically significant.

It is also shown that in specimens from both Boxgrove and Westbury Cave, when the effect of climate upon morphological variability within the Westbury *Microtus* faunas is

tested, specimens from stratigraphic levels associated with cooler conditions display reduced variance in both size and shape. All species display an increase in the tilt of the AC region and T4 and T5 towards the lingual surface of the tooth in warmer conditions. It is suggested that climate is not likely to have had a direct effect upon M_1 morphology, but that its effects on factors such predation, competition, maturation rate and mixing between populations may have indirectly influenced the amount of shape variance seen in the M_1.

The fact that a clear climatic signal can be seen in both size and shape independently of one another in *Microtus* M_1 teeth at Westbury suggests that the effect of climate upon the teeth of *Microtus* is both independent from and strong enough to overcome the allometric component within the datasets. This finding, along with those of Mointure and Brunet-Lecomte (2004) and McGuire (2009), suggest that an important implication of this finding is the potential for *Microtus* species to be used as a palaeoclimatic proxy in addition to standard methods of analysis such as the Mutual Climatic Range theory in Beetles and Molluscs (e.g. Moine et al., 2002; Elias, 2001) and climatic reconstruction using habitat preferences of mammalian species (e.g. Andrews, 1990).

Evaluation of the suitability of such methods to this type of material and to analysis of new information that can be gained through the application of this technique, as compared with more traditional metric measurements.

The analyses and conclusions presented within this study indicate that there are clear advantages in using GMM methods in analyses of *Microtus* M_1 teeth. The ability of these methods to distinguish between species is proved to be extremely accurate, and is of particular use in species which display very similar M_1 morphologies. There does not appear to be an adverse effect on the statistical significance of the results gained, of the ability to separate species when reduced areas of the tooth are examined. This means that these techniques could be of particular use in archaeological assemblages where samples are frequently damaged due to taphanomic factors. This study suggests that GMM methods may be of use in taxonomic studies of ancient material and results show that the taxonomic position of *M. arvalinus* should be revised and also have also brought into question the status of archaeological *M. subterraneus*, both results which have not previously been suggested by traditional metric measurements.

10.2 IMPLICATIONS FOR FURTHER RESEARCH

The implications of the results gained above should take future research in several directions. Firstly, the primary finding of this study is that GMM methods have considerable potential when used in the analysis of *Microtus* M_1 teeth. The ability of these methods to distinguish between closely related species is a significant improvement upon standard techniques and has the potential to be applied to other Microtine rodents within the archaeological record.

The understanding of the geographic and climatic effect upon M_1 morphology within this study has been hindered by the lack of specific locations and climatic information for all specimens included within the modern dataset. Further research investigating

change in M_1 morphology across geographical and climatic boundaries would allow for the interpretation of palaeontological samples to be better understood, and for the potential for *Microtus* M_1 remains to be used as a palaeoclimatic or palaeogeographic proxy to be evaluated in greater depth than then limitations of the current study have allowed.

This study identifies an extremely large and statistically significant difference between modern and Early Middle Pleistocene, that is possibly caused by convergent evolution or a genetic bottleneck may have occurred between the Early Middle Pleistocene and the present day. It is suggested that further investigation should take two forms; Firstly, comparing the morphology of modern *M. subterraneus* throughout the entire present-day range may provide indications of a population bottle neck or of a population which is similar morphologically to the Early Middle Pleistocene samples. Secondly, a systematic study of variance in *M. subterraneus* M_1 morphology through time may provide an indication of where and when *M. subterraneus* morphology diverged.

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APPENDIX A1: Modern sample

	ID	Country	Site
M. gregalis	14.11.1.97	USSR	Yenisii
M. gregalis	14.11.1.99	USSR	Yenisii
M. gregalis	14.11.1.98	USSR	Yenisii
M. gregalis	12.4.1.107	USSR	Altai mountains
M. gregalis	12.4.1.106	USSR	Altai mountains
M. gregalis	12.4.1.105	USSR	Altai mountains
M. gregalis	12.4.1.104	USSR	Altai mountains
M. gregalis	8.11.6.9	USSR	Altai mountains
M. gregalis	28.4.4.14	USSR	
M. gregalis	28.4.4.17	USSR	
M. gregalis	8.4.4.15	USSR	
M. gregalis	14.11.1.112	USSR	
M. gregalis	14.11.1.101	USSR	
M. gregalis	14.11.1.109	USSR	
M. gregalis	14.11.1.110	USSR	
M. gregalis	14.11.1.108	USSR	
M. gregalis	14.11.1.105	USSR	
M. gregalis	14.11.1.111	USSR	
M. gregalis	14.11.1.102	USSR	
M. gregalis	14.11.1.108	USSR	
M. gregalis	14.11.1.107	USSR	**Species**
M. gregalis	14.11.1.103	USSR	
M. gregalis	14.11.1.100	USSR	
M. gregalis	14.11.1.104	USSR	
M. gregalis	9.4.3.99		kashgar
M. gregalis	9.4.3.98		kashgar
M. gregalis	9.4.3.97		kashgar
M. gregalis	9.4.3.96		kashgar
M. gregalis	23.12.1.47	USSR	Altai mountains
M. gregalis	23.12.1.50	USSR	Altai mountains
M. gregalis	23.12.1.55	USSR	Altai mountains
M. gregalis	23.12.1.48	USSR	Altai mountains
M. gregalis	23.12.1.52	USSR	Altai mountains
M. gregalis	23.12.1.62	USSR	Altai mountains
M. gregalis	23.12.1.49	USSR	Altai mountains
M. gregalis	28.6.19.33	USSR	Transbikalia
M. gregalis	28.6.19.32	USSR	Transbikalia
M. gregalis	26.6.19.31	USSR	Transbikalia
M. gregalis	28.6.19.34	USSR	Transbikalia
M. gregalis	28.6.19.36	USSR	Transbikalia
M. gregalis	28.6.19.35	USSR	Transbikalia

Species	ID	Country	Site
M. subterraneus	64.281	France	Calais
M. subterraneus	64.282	France	Calais
M. subterraneus	64.275	France	Calais
M. subterraneus	64.276	France	Calais
M. subterraneus	64.283	France	Calais
M. subterraneus	64.277	France	Calais
M. subterraneus	64.278	France	Calais
M. subterraneus	64.28	France	Calais
M. subterraneus	64.279	France	Calais
M. subterraneus	64.274	France	Calais
M. subterraneus	62.1691	Switzerland	
M. subterraneus	62.1682	Switzerland	
M. subterraneus	56.144	Switzerland	
M. subterraneus	62.678	Switzerland	
M. subterraneus	62.1688	Switzerland	
M. subterraneus	62.169	Switzerland	
M. subterraneus	47.693	Switzerland	
M. subterraneus	50.146	Switzerland	
M. subterraneus	50.145	Switzerland	
M. subterraneus	62.1685	Switzerland	
M. subterraneus	50.147	Switzerland	
M. subterraneus	62.1684	Switzerland	
M. subterraneus	19.7.7.2189	Belgium	
M. subterraneus	?	Belgium	
M. subterraneus	137a	Belgium	
M. subterraneus	37.1.3.178	Belgium	
M. subterraneus		yugoslavia	
M. subterraneus		yugoslavia	
M. subterraneus		yugoslavia	
M. subterraneus		yugoslavia	
M. subterraneus		yugoslavia	
M. subterraneus		yugoslavia	
M. subterraneus		yugoslavia	
M. subterraneus		yugoslavia	
M. subterraneus		yugoslavia	
M. subterraneus		romania	
M. subterraneus		romania	
M. subterraneus		romania	
M. subterraneus		romania	
M. subterraneus		romania	
M. subterraneus		romania	
M. subterraneus		romania	
M. subterraneus	6.3.6.162	Asia Minor	
M. subterraneus	6.3.6.146	Asia Minor	

Species	ID	Country	Site
M. subterraneus	6.3.6.163	Asia Minor	
M. subterraneus	6.3.6.144	Asia Minor	
M. subterraneus	6.3.6.150	Asia Minor	
M. subterraneus	6.3.6.143	Asia Minor	
M. subterraneus	6.3.6.165	Asia Minor	
M. subterraneus	6.3.6.152	Asia Minor	
M. subterraneus	6.5.1.68	Asia Minor	
M. subterraneus	6.3.6.166	Asia Minor	
M. subterraneus	6.3.6.160	Asia Minor	
M. subterraneus	6.3.6.154	Asia Minor	
M. subterraneus	6.3.6.153	Asia Minor	
M. subterraneus	6.3.6.147	Asia Minor	
M. subterraneus	6.3.6.164	Asia Minor	
M. subterraneus	6.5.1.75	Asia Minor	
M. subterraneus	6.3.6.155	Asia Minor	
M. subterraneus	6.5.1.71	Asia Minor	
M. subterraneus	6.5.1.66	Asia Minor	
M. subterraneus	6.3.6.161	Asia Minor	
M. subterraneus	6.4.1.69	Asia Minor	
M. subterraneus	6.5.1.72	Asia Minor	
M. subterraneus	6.3.6.151	Asia Minor	
M. subterraneus	6.3.6.57	Asia Minor	
M. subterraneus	6.3.6.167	Asia Minor	
M. subterraneus	6.5.1.74	Asia Minor	
M. subterraneus	6.5.1.77	Asia Minor	
M. subterraneus	67.529	France	Calais
M. subterraneus	67.53	France	Calais
M. subterraneus	67.531	France	Calais
M. subterraneus	67.532	France	Calais
M. subterraneus	67.534	France	Calais
M. subterraneus	67.535	France	Calais
M. subterraneus	67.536	France	Calais
M. subterraneus	67.537	France	Calais
M. subterraneus	67.538	France	Calais
M. subterraneus	67.539	France	Calais
M. subterraneus	67.54	France	Calais
M. agrestis	8.8.4.227	France	
M. agrestis	8.8.4.230	France	
M. agrestis	45.7.5.7	France	
M. agrestis	8.8.4.232	France	
M. agrestis	8.8.4.229	France	
M. agrestis	8.8.4.251	France	
M. agrestis	8.8.4.228	France	

Species	ID	Country	Site
M. agrestis	?	France	
M. agrestis	1.11.7.12	France	
M. agrestis	34.6.22.28	France	
M. agrestis	8.8.7.16.3	France	
M. agrestis	83.523	France	
M. agrestis	62.1556	Switzerland	
M. agrestis	62.1558	Switzerland	
M. agrestis	62.1559	Switzerland	
M. agrestis	62.1548	Switzerland	
M. agrestis	62.1557	Switzerland	
M. agrestis	62.1536	Switzerland	
M. agrestis	62.1551	Switzerland	
M. agrestis	62.1553	Switzerland	
M. agrestis	62.1555	Switzerland	
M. agrestis	62.156	Switzerland	
M. agrestis	45.10.25.6	Sweden	
M. agrestis	o.5.15.5	Sweden	
M. agrestis	45.10.25.5	Sweden	
M. agrestis	0.5.15.4	Sweden	
M. agrestis	93.3.1.12	Sweden	
M. agrestis	50.89	Sweden	
M. agrestis	69.768	Sweden	
M. agrestis	0.5.15.3	Sweden	
M. agrestis	67.755	norway	
M. agrestis	67.756	UK	
M. agrestis	67.76	UK	
M. agrestis	67.758	UK	
M. agrestis	67.754	UK	
M. agrestis	?	UK	
M. agrestis	67.759	UK	
M. agrestis	1	UK	
M. agrestis	2	UK	
M. agrestis	3	UK	
M. agrestis	4	UK	
M. agrestis	5	UK	
M. agrestis	6	UK	
M. agrestis	7	UK	
M. agrestis	8	UK	
M. agrestis	9	UK	
M. agrestis	10	UK	
M. agrestis	11	UK	
M. agrestis	12	UK	

APPENDIX A2: Walou Cave sample

Species	ID	Stratigraphic level
M. Arvalis/agrestis	WA97 M14 B? 9 *19	B2 a B4
M. Arvalis/agrestis	WA97 M14 B? 9 *19	B2 a B4
M. Arvalis/agrestis	WA97 M14 B? 9 *19	B2 a B4
M. Arvalis/agrestis	WA00 J17 C6 1 *15	c1-1
M. Arvalis/agrestis	WA98 J20 C2 *6	c11-2
M. Arvalis/agrestis	WA98 J20 C2 *6	c11-2
M. Arvalis/agrestis	WA98 J20 C2 *6	c11-2
M. Arvalis/agrestis	WA98 J20 C2 *6	c11-2
M. Arvalis/agrestis	WA98 J20 C2 *6	c11-2
M. Arvalis/agrestis	WA97 M24 B? 8 *41	c11-2
M. Arvalis/agrestis	WA97 M24 A6 1 *32	c11-2
M. Arvalis/agrestis	WA00 L8 J17 2	c1-1
M. Arvalis/agrestis	WA97 E24 CSUP 1 *36	c1-6
M. Arvalis/agrestis	WA00 J17 C7B *13	c1-6
M. Arvalis/agrestis	WA97 E24 CSUP 2 *20	c1-8
M. Arvalis/agrestis	WA99 J18 B5 *3	B-B5
M. Arvalis/agrestis	wa97 cBRUNCLAIR 10 2+3	c11-4
M. Arvalis/agrestis	WA97 M24 B? 9	B-B2-B4
M. Arvalis/agrestis	WA97 M24 B? 9	B-B2-B4
M. Arvalis/agrestis	WA97 M24 B? 9	B-B2-B4
M. Arvalis/agrestis	WA97 014 DA 22	C4/ D
M. Arvalis/agrestis	WA97 014 DA 22	C4/ D
M. Arvalis/agrestis	WA97 014 DA 22	C4/ D
M. Arvalis/agrestis	WA97 014 DA 22	C4/ D
M. Arvalis/agrestis	WA97 014 DA 22	C4/ D
M. Arvalis/agrestis	WA97 014 CFONE 2 5+6	C11-6
M. Arvalis/agrestis	WA97 014 CFONE 2 5+6	C11-6
M. Arvalis/agrestis	WA97 M24 B? 10	B-B2-B4
M. Arvalis/agrestis	WA97 M24 B? 10	B-B2-B4
M. Arvalis/agrestis	WA97 M24 B? 10	B-B2-B4
M. Arvalis/agrestis	WA97 M24 B? 10	B-B2-B4
M. Arvalis/agrestis	WA97 ED4 CSUP 6	C1-8
M. Arvalis/agrestis	WA97 ED4 CSUP 6	C1-8
M. Arvalis/agrestis	WA97 ED4 CSUP 6	C1-8
M. Arvalis/agrestis	WA97 ED4 CSUP 6	C1-8
M. Arvalis/agrestis	WA97 ED4 CSUP 6	C1-8
M. Arvalis/agrestis	WA97 ED4 CSUP 6	C1-8
M. Arvalis/agrestis	WA97 014 DA 23	C4/ D
M. Arvalis/agrestis	WA97 014 DA 23	C4/ D
M. Arvalis/agrestis	WA97 014 DA 23	C4/ D
M. Arvalis/agrestis	WA97 G21 CSUP 1	C1-8
M. Arvalis/agrestis	WA97 G21 CSUP 1	C1-8

APPENDIX A3: Boxgrove sample

Species	ID	Level
M. arvalis/ agrestis	BX Q2 GTP17 4c BS87-119 1	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS87-119 2	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS87-119 3	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS87-119 4	4c
P.arvalodies	BX Q2 GTP17 4c BS87-119 5	4c
p. arvaloides	BX Q2 GTP17 4c BS87-119 6	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS87-119 7	4c
p. arvaloides	BX Q2 GTP17 4c BS87-119 8	4c
p. arvaloides	BX Q2 GTP17 4c BS87-119 9	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS87-119 10	4c
p. arvaloides	BX Q2 GTP17 4c BS87-119 11	4c
p. arvaloides	BX Q2 GTP17 4c BS87-119 12	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-56 1	4c
p. arvaloides	BX Q2 GTP17 4c BS86-56 2	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-56 3	4c
M.oeconomus	BX Q2 GTP17 5c BS90-1130 1	5c
M. arvalis/ agrestis	BX Q2 GTP17 13 5a 86-84 1	5c
M. arvalis/ agrestis	BX Q2 GTP17 13 5a 86-84 2	5c
M. arvalis/ agrestis	BX Q2 GTP17 13 5a 86-84 3	5c
p. arvaloides	BX Q2 '17 5a BS86-25 1	5a
p. arvaloides	BX Q2 '17 5a BS86-25 2	5a
M. arvalis/ agrestis	BX Q2 '17 5a 86-76 1	5a
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-27 1	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-27 2	4c
p. arvaloides	BX Q2 GTP17 4c BS86-27 3	4c
p. arvaloides	BX Q2 GTP17 4c BS86-27 4	4c
p. arvaloides	BX Q2 GTP17 4c BS86-27 5	4c
p. arvaloides	BX Q2 GTP17 4c BS86-27 6	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-27 7	4c
p. arvaloides	BX Q2 GTP17 4c BS86-27 8	4c
p. arvaloides	BX Q2 GTP17 4 4c BS86-70 1	4c
p. arvaloides	BX Q2 GTP17 4 4c BS86-70 2	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-20 1	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-26 1	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-26 2	4c

Species	ID	Level
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-26 3	4c
p. arvaloides	BX Q2 GTP17 4c BS86-26 4	4c
M.arvaloidiens	BX Q2 GTP17 4c BS86-26 5	4c
p. arvaloides	BX Q2 GTP17 4c BS86-26 6	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-26 7	4c
p. arvaloides	BX Q2 GTP17 4c BS86-26 8	4c
M. arvalis/ agrestis	BX Q2 GTP17 4c BS86-26 9	4c
M. arvalis/ agrestis	BX Q2 '20 4c 87-258 3	4c
M. arvalis/ agrestis	BX Q1b 54d 5a BS87-133 1	5a
m. gregalis	BX Q1b 54d 5a BS87-133 2	5a
M. arvalis/ agrestis	BX Q1b 54d 5a BS87-133 3	5a
M. arvalis/ agrestis	BX 1B 5a 88-502 1	5a
p. arvaloides	BX 1B 5a 88-502 2	5a
p. arvaloides	BX 1B 5a 88-502 3	5a
M. arvalis/ agrestis	BX Q1b 50e 5a BS87-132 1	5a
p. arvaloides	BX Q2 GTP17 16 5a BS86-82 1	5a
p. arvaloides	BX Q2 GTP17 5a 86-75 1	5a
p. arvaloides	BX Q2 GTP17 5a 86-75 2	5a
p. arvaloides	BX Q2 GTP17 5a 86-75 3	5a
p. arvaloides	BX Q2 GTP17 5a 86-75 4	5a
p. arvaloides	BX Q1b 4d 89-1005 1	4d
M. arvalis/ agrestis	BX Q1b 4d 89-1005 2	4d
P. arvaloides	BX Q2 '20 4c 87-258 1	4c
P. arvaloides	BX Q2 '20 4c 87-258 2	4c
M. oeconomus	BX BS 86-42 1	4c
P. arvaloides	BX BS 86-42 2	4c
M. oeconomus	BX BS 86-42 3	4c
P. arvaloides	BX Q2 GTP13 3 87-109 1	3
P. arvaloides	BX Q2 GTP13 3 87-109 2	3
P. arvaloides	BX Q2 GTP13 3 87-109 3	3
M. arvalis/ agrestis	BX Q2 GTP13 3 87-109 4	3
M. arvalis/ agrestis	BX Q2 GTP13 3 87-109 5	3
M. arvalis/ agrestis	BX Q2 GTP13 3 87-109 6	3
M. arvalis/ agrestis	BX Q2 GTP13 3 87-109 7	4
M. arvaloidens	BX Q2 5b 86-46 1	5b
M. arvaloidens	BX Q2 SEP2 5b BS86-49 1	5b
M. arvalis/ agrestis	BX Q2 SEP2 5b BS86-49 1	5b
M. arvaloidens	BX Q2 EPQ TP4 5b 90-1165 1	5b
M. arvaloidens	BX Q2 EPQ TP4 5b 90-1165 2	5b
P. arvaloides	BX Q2 EPQ TP4 5b 90-1165 3	5b
P. arvaloides	BX Q2 EPQ TP4 5b 90-1165 4	5b
M. arvalis/ agrestis	BX Q2 EPQ TP4 5b 90-1165 5	5b
P. arvaloides	BX Q2 5b 86-38 1	5b
M. arvaloidens	BX Q2 4c 87-100 1	4c

Species	ID	Level
P. arvaloides	BX Q2 4c 87-100 2	4c
M. arvalis/ agrestis	BX Q2 4c 87-100 3	4c
P. arvaloides	BX Q2 4c 87-100 4	4c
M. arvalis/ agrestis	BX Q2 4c 87-100 5	4c
M. arvalis/ agrestis	BX Q2 4c 87-100 6	4c
M. arvalis/ agrestis	BX Q2 4c 87-100 7	4c
M. arvalis/ agrestis	BX Q2 4c 87-100 8	4c
m. gregalis	BX Q2 4c 87-100 9	4c
P. arvaloides	BX Q2 4c 87-100 10	4c
P. arvaloides	BX Q2 4c 87-100 11	4c
P. arvaloides	BX Q2 4c 87-100 12	4c
P. arvaloides	BX Q2 4c 87-100 13	4c
P. arvaloides	BX Q2 4c 87-100 14	4c
P. arvaloides	BX Q2 4c 87-100 15	4c
P. arvaloides	BX Q2 4c 87-100 16	4c
M. arvaloidens	BX 4c 87-251 1	4c
M. arvalis/ agrestis	BX 4c 87-251 2	4c
M. arvalis/ agrestis	BX 4c 87-251 3	4c
P. arvaloides	BX 4c 87-251 4	4c
M. oeconomus	BX 4c 87-251 5	4c
P. arvaloides	BX 4c 87-251 6	4c
P. arvaloides	BX 4c 87-251 7	4c
P. arvaloides	BX 4c 87-251 8	4c
M. arvaloidens	BX 4c 87-251 9	4c
M. arvalis/ agrestis	BX 4c 87-251 10	4c
P. arvaloides	BX 4c 87-251 11	4c
P. arvaloides	BX 4c 87-251 12	4c
M. arvalis/ agrestis	BX 4c 87-251 13	4c
P. arvaloides	BX 4c 87-251 14	4c
P. arvaloides	BX 4c 87-251 15	4c
M. arvaloidens	BX 4c 87-251 16	4c
P. arvaloides	BX 4c 87-251 17	5
M. arvalis/ agrestis	BX 4c 87-251 18	5
P. arvaloides	BX 4c 87-251 19	5
M. arvalis/ agrestis	BX 4c 87-251 20	5
M. arvalis/ agrestis	BX 4c 87-251 21	5
P. arvaloides	BX 4c 87-251 22	5
P. arvaloides	BX 4c 87-251 23	5
M. arvalis/ agrestis	BX Q2 GTP3 34 4c 884-61 3	2
P. arvaloides	BX Q2 GTP3 34 4c 884-61 4	2
P. arvaloides	BX Q2 GTP3 34 4c 884-61 5	2
P. arvaloides	BX Q2 GTP3 34 4c 884-61 6	2
M. arvalis/ agrestis	BX Q2 GTP3 34 4c 884-61 7	2
P. arvaloides	BX Q2 GTP3 34 4c 884-61 8	2

Species	ID	Level
P. arvaloides	BX Q2 GTP3 4c BS87-124 1	4c
M. arvalis/ agrestis	BX Q2 GTP3 4c BS87-124 2	4c
P. arvaloides	BX Q2 GTP3 4c BS87-124 3	4c
M. arvalis/ agrestis	BX Q2 GTP3 4c BS87-124 4	4c
P. arvaloides	BX Q2 GTP3 4c BS87-124 5	4c
P. arvaloides	BX Q2 GTP3 4c BS87-124 6	4c
P. arvaloides	BX Q2 GTP3 4c BS87-124 7	4c
M. arvalis/ agrestis	BX Q2 GTP3 4b 3 90-1365 1	4b
P. arvaloides	BX Q2 GTP3 4b 3 90-1365 2	4b
M. gregalis	BX A Q2 '17 BS86-76 1	5a
M. arvalis/ agrestis	BX A Q1b 6 B87-120 1	6
M. arvalis/ agrestis	BX A Q1b 6 B87-120 2	6
M. arvalis/ agrestis	BX A Q1b 6 B87-120 3	6
p. arvaloides	BX A Q1b 6 B87-120 4	6
M. arvalis/ agrestis	BX A Q1b 6 B87-120 5	6
M. arvalis/ agrestis	BX A Q1b 6 B87-120 6	6
M. arvalis/ agrestis	BX A Q1b 6 B87-120 7	6
M. arvalis/ agrestis	BX A Q1b 6 B87-120 8	6
M. arvalis/ agrestis	BX A Q1b 6 B87-120 9	6
M. arvalis/ agrestis	BX A Q1b 6 B87-120 10	6
p. arvaloides	BX A Q1b 6 B87-120 11	6
M. arvalis/ agrestis	BX A Q1 6 SM255 1	6
P. gregaloides	BX A Q1 6 SM255 2	6
p. arvaloides	BX A Q1 6 SM255 3	6
p. arvaloides	BX A Q1 6 SM255 4	6
p. arvaloides	BX A Q1 6 SM255 5	6
M. arvalis/ agrestis	BX Q1 GTP16 4c BS86-24 1	6
p. arvaloides	BX Q1a 4c BS90-1152 1	4c
p. arvaloides	BX Q1a 6 BS90-1138 1	6
p. arvaloides	BX Q1 GTP15 4c BS86-16 1	4c
M. arvalis/ agrestis	BX Q1 GTP15 4c BS86-16 2	4c
M. arvalis/ agrestis	BX Q1 GTP15 4c BS86-16 3	4c
p. arvaloides	BX Q1 GTP15 4c BS86-16 4	4c
M. arvalis/ agrestis	BX Q2 120 6 86-54 1	6
M. arvalis/ agrestis	BX Q2 120 6 86-54 2	6
M. arvalis/ agrestis	BX Q2 120 6 86-54 3	6
M. arvalis/ agrestis	BX Q2 120 6 86-54 4	6
M. arvalis/ agrestis	BX Q2 120 6 86-54 5	6
M. arvalis/ agrestis	BX Q2 120 6 86-54 6	6
p. arvaloides	BX Q2 GTP20 4c 87-258 1	4c
p. arvaloides	BX Q2 GTP20 4c 87-258 2	4c
M. arvalis/ agrestis	BX Q2b 5a BS87-99 1	5a
p. arvaloides	BX Q2b 5a BS87-99 2	5a
p. arvaloides	BX Q2b 5a BS87-99 3	5a
p. arvaloides	BX Q2b 5a BS87-99 4	5a

APPENDIX A4: Westbury sample

Species	ID	Stratigraphic level
P. gregaloides	WSM78 W9 13 1	WSM78 W9 13
P. gregaloides	WSM78 W9 13 2	WSM78 W9 13
P. gregaloides	WSM78 W9 13 3	WSM78 W9 13
P. gregaloides	WSM78 W9 13 4	WSM78 W9 13
P. gregaloides	WSM78 W9 13 5	WSM78 W9 13
M. arvalis/ agrestis	WSM78 W9 13 6	WSM78 W9 13
M. arvalis/ agrestis	WSM78 W9 13 7	WSM78 W9 13
M. arvalis/ agrestis	WSM78 W9 13 8	WSM78 W9 13
P. gregaloides	WSM78 W9 13 9	WSM78 W9 13
P. gregaloides	WSM78 W9 13 10	WSM78 W9 13
P. gregaloides	WSM78 W9 13 11	WSM78 W9 13
P. gregaloides	WSM78 W9 13 12	WSM78 W9 13
P. gregaloides	WSM78 W9 11/12 1	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 2	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 3	WSM78 W9 11/12
M. oeconomus	WSM78 W9 11/12 4	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 5	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 6	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 7	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 8	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 9	WSM78 W9 11/12
M. arvalis/ agrestis	WSM78 W9 11/12 10	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 11	WSM78 W9 11/12
P. gregaloides	WSM78 W9 11/12 12	WSM78 W9 11/12
P. gregaloides	WSM78 W9 12 1	WSM78 W9 12
M. arvalis/ agrestis	WSM78 W9 12 2	WSM78 W9 12
P. gregaloides	WSM78 W9 12 3	WSM78 W9 12
P. gregaloides	WSM78 W9 12 4	WSM78 W9 12
P. gregaloides	WSM78 W9 12 5	WSM78 W9 12
M. arvalis/ agrestis	WSM78 W9 12 6	WSM78 W9 12
P. gregaloides	WSM78 W9 12 7	WSM78 W9 12
P. arvalodies	WSM78 W9 12 8	WSM78 W9 12
P. gregaloides	WSM78 W9 12 9	WSM78 W9 12
P. gregaloides	WSM78 W2 36 1	WSM78 W2 36
P. gregaloides	WSM78 W2 36 2	WSM78 W2 36
P. gregaloides	WSM78 W2 36 3	WSM78 W2 36
P. gregaloides	WSM78 W2 36 4	WSM78 W2 36
P. gregaloides	WSM78 W2 36 5	WSM78 W2 36

Species	ID	Stratigraphic level
P. gregaloides	WSM78 W2 36 11	WSM78 W2 36
P. gregaloides	WSM78 W2 36 12	WSM78 W2 36
P. gregaloides	WSM78 W2 36 13	WSM78 W2 36
M. oeconomus	WSM78 W2 36 14	WSM78 W2 36
P. gregaloides	WSM78 W2 36 15	WSM78 W2 36
P. arvalodies	WSM78 W2 36 16	WSM78 W2 36
P. gregaloides	WSM78 W2 36 17	WSM78 W2 36
P. gregaloides	WSM78 W2 36 18	WSM78 W2 36
P. gregaloides	WSM78 W2 36 19	WSM78 W2 36
P. gregaloides	WSM78 W2 36 20	WSM78 W2 36
M. oeconomus	WSM78 W2 36 21	WSM78 W2 36
M. arvalis/ agrestis	WSM78 W2 22 1	WSM78 W2 22
P. arvalodies	WSM78 W2 22 2	WSM78 W2 22
P. arvalodies	WSM78 W2 22 3	WSM78 W2 22
M. oeconomus	WSM78 W2 72 1	WSM78 W2 72
M. arvalis/ agrestis	WSM78 W2 72 2	WSM78 W2 72
M. arvalis/ agrestis	WSM78 W2 72 3	WSM78 W2 72
M. oeconomus	WSM78 W2 72 4	WSM78 W2 72
M. arvalis/ agrestis	WSM78 W2 72 5	WSM78 W2 72
M. arvalis/ agrestis	WSM78 W2 72 6	WSM78 W2 72
M. oeconomus	WSM78 W2 72 7	WSM78 W2 72
P. arvalodies	WSM78 W2 72 8	WSM78 W2 72
M. arvalis/ agrestis	WSM78 W2 72 9	WSM78 W2 72
P. arvalodies	WSM78 W2 72 10	WSM78 W2 72
M. oeconomus	WSM78 W2 72 11	WSM78 W2 72
M. arvalis/ agrestis	WSM78 W2 64 1	WSM78 W2 64
M. oeconomus	WSM78 W2 64 2	WSM78 W2 64
M. arvalis/ agrestis	WSM78 W2 64 3	WSM78 W2 64
M. oeconomus	WSM78 W2 64 4	WSM78 W2 64
M. arvalis/ agrestis	WSM78 W2 64 5	WSM78 W2 64
M. oeconomus	WSM78 W2 64 6	WSM78 W2 64
M. arvalis/ agrestis	WSM78 W2 64 7	WSM78 W2 64
M. oeconomus	WSM78 W2 64 8	WSM78 W2 64
M. arvalis/ agrestis	WSM78 W2 21 1	WSM78 W2 21
M. arvalis/ agrestis	WSM78 W2 21 2	WSM78 W2 21
P. arvalodies	WSM78 W2 21 3	WSM78 W2 21
M. arvalis/ agrestis	WSM78 W2 21 4	WSM78 W2 21
M. oeconomus	WSM78 W2 21 5	WSM78 W2 21
P. arvalodies	WSM78 W2 21 6	WSM78 W2 21
M. arvalis/ agrestis	WSM78 W2 21 7	WSM78 W2 21
P. arvalodies	WSM78 W2 21 8	WSM78 W2 21
M. arvalis/ agrestis	WSM78 W2 21 9	WSM78 W2 21
P. arvalodies	WSM78 W2 21 10	WSM78 W2 21

Species	ID	Stratigraphic level
P. arvalodies	WSM78 W2 21 11	WSM78 W2 21
P. arvalodies	WSM78 W2 21 12	WSM78 W2 21
M. arvalis/ agrestis	WSM78 W2 21 13	WSM78 W2 21
P. arvalodies	WSM78 W2 21 14	WSM78 W2 21
M. arvalis/ agrestis	WSM78 W2 77 1	WSM78 W2 77
M. arvalis/ agrestis	WSM78 W2 77 2	WSM78 W2 77
M. arvalis/ agrestis	WSM78 W2 77 3	WSM78 W2 77
P. arvalodies	WSM78 W2 77 4	WSM78 W2 77
M. arvalis/ agrestis	WSM78 W2 68 1	WSM78 W2 68
M. oeconomus	WSM78 W2 68 2	WSM78 W2 68
M. arvalis/ agrestis	WSM78 W2 68 3	WSM78 W2 68
M. oeconomus	WSM78 W2 68 4	WSM78 W2 68
M. arvalis/ agrestis	WSM78 W2 68 5	WSM78 W2 68
M. arvalis/ agrestis	WSM78 W2 68 6	WSM78 W2 68
P. arvalodies	WSM78 W2 68 7	WSM78 W2 68
M. arvalis/ agrestis	WSM78 W2 68 8	WSM78 W2 68
M. arvalis/ agrestis	WSM78 W2 68 9	WSM78 W2 68
M. arvalis/ agrestis	WSM78 W2 68 10	WSM78 W2 68
M. arvalis/ agrestis	WSM78 W2 68 11	WSM78 W2 68
P. arvalodies	WSM78 W2 68 12	WSM78 W2 68
M. arvalis/ agrestis	WSM78 W2 68 13	WSM78 W2 68
P. gregaloides	WSM79 W2/9 184 1	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 2	WSM79 W2/9 184
p. arvaloides	WSM79 W2/9 184 3	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 4	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 5	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 6	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 7	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 8	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 9	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 10	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 11	WSM79 W2/9 184
M. arvalis/ agrestis	WSM79 W2/9 184 12	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 13	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 14	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 15	WSM79 W2/9 184
M. arvalis/ agrestis	WSM79 W2/9 184 16	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 17	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 18	WSM79 W2/9 184
p. arvaloides	WSM79 W2/9 184 19	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 20	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 21	WSM79 W2/9 184
p. arvaloides	WSM79 W2/9 184 22	WSM79 W2/9 184

Species	ID	Stratigraphic level
p. arvaloides	WSM79 W2/9 184 23	WSM79 W2/9 184
p. arvaloides	WSM79 W2/9 184 24	WSM79 W2/9 184
P. gregaloides	WSM79 W2/9 184 25	WSM79 W2/9 184
p. arvaloides	WSM79 W2/9 184 26	WSM79 W2/9 184
P. gregaloides	WSM78 W9 50 1	WSM78 W9 50
M. arvalis/ agrestis	WSM78 W9 50 2	WSM78 W9 50
P. gregaloides	WSM78 W9 50 3	WSM78 W9 50
P. gregaloides	WSM78 W9 50 4	WSM78 W9 50
P. gregaloides	WSM78 W9 50 5	WSM78 W9 50
P. gregaloides	WSM78 W9 50 6	WSM78 W9 50
P. gregaloides	WSM78 W9 50 7	WSM78 W9 50
P. gregaloides	WSM78 W9 50 8	WSM78 W9 50
P. gregaloides	WSM78 W9 50 9	WSM78 W9 50
P. gregaloides	WSM78 W9 50 10	WSM78 W9 50
P. gregaloides	WSM78 W9 50 11	WSM78 W9 50
P. gregaloides	WSM78 W9 50 12	WSM78 W9 50
P. gregaloides	WSM78 W9 50 13	WSM78 W9 50
M. arvalis/ agrestis	WSM78 W9 50 14	WSM78 W9 50
P. gregaloides	WSM78 W9 50 15	WSM78 W9 50
M. arvalis/ agrestis	WSM78 W9 50 16	WSM78 W9 50
P. gregaloides	WSM78 W9 50 17	WSM78 W9 50
P. gregaloides	WSM78 W9 50 18	WSM78 W9 50
P. gregaloides	WSM78 W9 50 19	WSM78 W9 50
M. arvalis/ agrestis	WSM78 W9 50 20	WSM78 W9 50
P. gregaloides	WSM78 W9 50 21	WSM78 W9 50
P. gregaloides	WSM78 W9 50 22	WSM78 W9 50
P. gregaloides	WSM78 W9 50 23	WSM78 W9 50
P. gregaloides	WSM78 W9 50 24	WSM78 W9 50
P. gregaloides	WSM78 W9 50 25	WSM78 W9 50
P. gregaloides	WSM78 W9 50 26	WSM78 W9 50
M. arvalis/ agrestis	WSM78 W9 57 1	WSM78 W9 57
M. arvalis/ agrestis	WSM78 W9 57 2	WSM78 W9 57
M. arvalis/ agrestis	WSM78 W9 57 3	WSM78 W9 57
M. arvalis/ agrestis	WSM78 W9 57 4	WSM78 W9 57
M. arvalis/ agrestis	WSM78 W9 57 5	WSM78 W9 57
M. arvalis/ agrestis	WSM78 W9 57 6	WSM78 W9 57
M. arvalis/ agrestis	WSM79 W9 5 1	WSM78 W9 5
M. arvalis/ agrestis	WSM79 W9 5 2	WSM78 W9 5
M. arvalis/ agrestis	WSM79 W9 5 3	WSM78 W9 5
M. arvalis/ agrestis	WSM79 W9 5 4	WSM78 W9 5
M. arvalis/ agrestis	WSM79 W2/9 135 1	WSM79 W2/9 135
M. arvalis/ agrestis	WSM78 W9 30 1	WSM78 W9 30
M. arvalis/ agrestis	WSM78 W9 30 2	WSM78 W9 30
M. oeconomus	WSM77 W5 99 1	WSM77 W5 99

Species	ID	Stratigraphic level
M. arvalis/ agrestis	WSM77 W5 99 2	WSM77 W5 99
M. arvalis/ agrestis	WSM77 W5 99 3	WSM77 W5 99
p. gregaloides	WSM77 W5 59 1	WSM77 W5 59
p. gregaloides	WSM77 W5 59 2	WSM77 W5 59
p. gregaloides	WSM77 W5 59 3	WSM77 W5 59
p. gregaloides	WSM77 W5 59 4	WSM77 W5 59
p. gregaloides	WSM77 W5 79 1	WSM77 W5 79
P. arvaloides	WSM77 W5 79 2	WSM77 W5 79
M. arvalis/ agrestis	WSM77 W5 79 3	WSM77 W5 79
P. arvaloides	WSM77 W5 79 4	WSM77 W5 79
P. arvaloides	WSM77 W5 79 5	WSM77 W5 79
P. arvaloides	WSM77 W5 79 6	WSM77 W5 79
M. oeconomus	WSM77 W5A3 35 1	WSM77 W5A3 35
p. gregaloides	WSM77 W5A3 35 2	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 3	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 4	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 5	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 6	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 7	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 8	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 9	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 10	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 11	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 12	WSM77 W5A3 35
M. arvalis/ agrestis	WSM77 W5A3 35 13	WSM77 W5A3 35
M. oeconomus	WSM77 W5 93 1	WSM77 W5 93
M. arvalis/ agrestis	WSM77 W5 93 2	WSM77 W5 93
M. arvalis/ agrestis	WSM77 W5 93 3	WSM77 W5 93
P. gregaloides	WSM78 W5 5 1	WSM78 W5 5
P. gregaloides	WSM78 W5 5 2	WSM78 W5 5
P. gregaloides	WSM78 W5 5 3	WSM78 W5 6
P. gregaloides	WSM78 W5 5 4	WSM78 W5 7
P. gregaloides	WSM78 W5 5 5	WSM78 W5 8
P. gregaloides	WSM78 W5 5 6	WSM78 W5 9
P. gregaloides	WSM78 W5 5 7	WSM78 W5 10
P. gregaloides	WSM78 W5 5 8	WSM78 W5 11
P. gregaloides	WSM78 W5 5 9	WSM78 W5 12
P. gregaloides	WSM78 W5 5 10	WSM78 W5 13
P. gregaloides	WSM78 W5 5 11	WSM78 W5 14
P. gregaloides	WSM78 W5 5 12	WSM78 W5 15
P. gregaloides	WSM78 W5 5 13	WSM78 W5 16
P. gregaloides	WSM78 W5 5 14	WSM78 W5 17
P. gregaloides	WSM78 W5 5 15	WSM78 W5 18
P. gregaloides	WSM78 W5 5 16	WSM78 W5 19

Species	ID	Stratigraphic level
P. gregaloides	WSM78 W5 5 17	WSM78 W5 20
P. gregaloides	WSM78 W5 5 18	WSM78 W5 21
P. gregaloides	WSM78 W5R3 170 1	WSM78 W5R3 170
P. gregaloides	WSM78 W5R3 170 2	WSM78 W5R3 170
P. gregaloides	WSM78 W5R3 170 3	WSM78 W5R3 170
P. gregaloides	WSM78 W5R3 170 4	WSM78 W5R3 170
P. gregaloides	WSM78 W5R3 170 5	WSM78 W5R3 170
P. gregaloides	WSM78 W5R3 170 6	WSM78 W5R3 170
P. gregaloides	WSM78 W5R3 170 7	WSM78 W5R3 170
P. gregaloides	WSM78 W5R3 170 8	WSM78 W5R3 171
P. gregaloides	WSM78 W5R3 170 9	WSM78 W5R3 172
P. gregaloides	WSM78 W5R3 170 10	WSM78 W5R3 173
P. gregaloides	WSM78 W5R3 170 11	WSM78 W5R3 174
P. gregaloides	WSM78 W5R3 170 12	WSM78 W5R3 175
P. gregaloides	WSM78 W5R3 170 13	WSM78 W5R3 176
P. gregaloides	WSM78 W5R3 170 14	WSM78 W5R3 177
P. gregaloides	WSM78 W5R3 170 15	WSM78 W5R3 178
P. gregaloides	WSM78 W5R3 170 16	WSM78 W5R3 179
P. gregaloides	WSM78 W5R3 170 17	WSM78 W5R3 180
P. gregaloides	WSM78 W5R3 170 18	WSM78 W5R3 181
P. gregaloides	WSM78 W5R3 170 19	WSM78 W5R3 182
P. gregaloides	WSM78 W5R3 170 20	WSM78 W5R3 183
P. gregaloides	WSM78 W5R3 170 21	WSM78 W5R3 184
P. gregaloides	WSM78 W5R3 170 22	WSM78 W5R3 185
P. gregaloides	WSM78 W5R3 170 23	WSM78 W5R3 186
P. gregaloides	WSM78 W5R3 170 24	WSM78 W5R3 187
P. gregaloides	WSM78 W5R3 170 25	WSM78 W5R3 188
P. gregaloides	WSM78 W5R3 170 26	WSM78 W5R3 189
P. gregaloides	WSM78 W5R3 170 27	WSM78 W5R3 190
P. gregaloides	WSM78 W5R3 170 28	WSM78 W5R3 191
P. gregaloides	WSM78 W5R3 170 29	WSM78 W5R3 192
P. gregaloides	WSM78 W5R3 170 30	WSM78 W5R3 193
P. gregaloides	WSM78 W5R3 170 31	WSM78 W5R3 194
P. gregaloides	WSM78 W5R3 170 32	WSM78 W5R3 195
M. oeconomus	WSM77 W5R3 153 1	WSM77 W5R3 153
M. oeconomus	WSM77 W5R3 153 2	WSM77 W5R3 153
M. oeconomus	WSM77 W5R3 153 3	WSM77 W5R3 153
M. oeconomus	WSM77 W5R3 170 1	WSM77 W5R3 170
M. arvalis/ agrestis	WSM77 W5R3 153 4	WSM77 W5R3 153
M. arvalis/ agrestis	WSM77 W5R3 153 5	WSM77 W5R3 153
M. arvalis/ agrestis	WSM77 W5R3 153 6	WSM77 W5R3 153
M. arvalis/ agrestis	WSM77 W5R3 153 7	WSM77 W5R3 153
M. arvalis/ agrestis	WSM77 W5 5 1	WSM77 W5 5
M. arvalis/ agrestis	WSM77 W5 5 2	WSM77 W5 5
M. arvalis/ agrestis	WSM77 W5 5 3	WSM77 W5 5

Species	ID	Stratigraphic level
M. arvalis/ agrestis	WSM77 W5R3 170 1	WSM77 W5R3 170
M. arvalis/ agrestis	WSM77 W5R3 170 2	WSM77 W5R3 170
M. arvalis/ agrestis	WSM77 W5 128 1	WSM77 W5 128
M. arvalis/ agrestis	WSM77 W5 128 2	WSM77 W5 128
M. arvalis/ agrestis	WSM77 W5 100 1	WSM77 W5 100
M. arvalis/ agrestis	WSM77 W5 100 2	WSM77 W5 100
M. arvalis/ agrestis	WSM77 W5 100 3	WSM77 W5 100
M. arvalis/ agrestis	WSM77 W5 100 4	WSM77 W5 100
M. arvalis/ agrestis	WSM77 W5 100 5	WSM77 W5 100
M. arvalis/ agrestis	WSM77 W5 100 6	WSM77 W5 100
M. arvalis/ agrestis	WSM77 W5 100 7	WSM77 W5 100
M. arvalis/ agrestis	WSM77 W5 160 1	WSM77 W5 160
M. arvalis/ agrestis	WSM77 W5E3 73 1	WSM77 W5E3 73
M. arvalis/ agrestis	WSM77 W5E3 73 2	WSM77 W5E3 73
M. arvalis/ agrestis	WSM77 W5E3 73 3	WSM77 W5E3 73
M. arvalis/ agrestis	WSM77 W5E3 73 4	WSM77 W5E3 73
M. arvalis/ agrestis	WSM77 W5E3 73 5	WSM77 W5E3 73
M. arvalis/ agrestis	WSM77 W5E3 73 6	WSM77 W5E3 73
M. arvalis/ agrestis	WSM77 W5E3 73 7	WSM77 W5E3 73
M. arvalis/ agrestis	WSM77 W5E3 73 8	WSM77 W5E3 73
M. oeconomus	WSM77 W5E3 73 9	WSM77 W5E3 73
P. gregaloides	WSM80 W5 27 1	WSM80 W5 27
P. gregaloides	WSM80 W5 27 2	WSM80 W5 27
P. gregaloides	WSM80 W5 27 3	WSM80 W5 27
P. gregaloides	WSM80 W5 27 4	WSM80 W5 27
P. gregaloides	WSM80 W5 27 5	WSM80 W5 27
P. gregaloides	WSM80 W5 27 6	WSM80 W5 27
P. gregaloides	WSM80 W5 27 7	WSM80 W5 27
P. gregaloides	WSM80 W5 27 8	WSM80 W5 27
M. arvalis/ agrestis	WSM80 W5 27 9	WSM80 W5 27
P. gregaloides	WSM80 W5 33 1	WSM80 W5 33
P. gregaloides	WSM80 W5 33 2	WSM80 W5 33
P. gregaloides	WSM80 W5 33 3	WSM80 W5 33
P. gregaloides	WSM80 W5 33 4	WSM80 W5 33
P. gregaloides	WSM80 W5 33 5	WSM80 W5 33
P. gregaloides	WSM80 W5 33 6	WSM80 W5 33
P. gregaloides	WSM80 W5 33 7	WSM80 W5 33
P. gregaloides	WSM80 W5 33 8	WSM80 W5 33
M. arvalis/ agrestis	WSM80 W5 33 9	WSM80 W5 33
P. gregaloides	WSM80 W5 33 10	WSM80 W5 33
P. gregaloides	WSM78 W9 159 1	WSM78 W9 159
P. gregaloides	WSM78 W9 159 2	WSM78 W9 159
P. gregaloides	WSM78 W9 159 3	WSM78 W9 159
P. gregaloides	WSM78 W9 159 4	WSM78 W9 159

Species	ID	Stratigraphic level
P. gregaloides	WSM78 W9 159 5	WSM78 W9 159
M. arvalis/ agrestis	WSM78 W9 159 6	WSM78 W9 159
P. gregaloides	WSM78 W9 159 7	WSM78 W9 159
P. gregaloides	WSM78 W9 159 8	WSM78 W9 159
M. arvalis/ agrestis	WSM78 W9 159 9	WSM78 W9 159
P. gregaloides	WSM78 W9 159 10	WSM78 W9 159
M. arvalis/ agrestis	WSM78 W9 159 11	WSM78 W9 159
M. arvalis/ agrestis	WSM78 W9 159 12	WSM78 W9 159
P. gregaloides	WSM78 W9 159 13	WSM78 W9 159
M. arvalis/ agrestis	WSM78 W9 159 14	WSM78 W9 159
M. arvalis/ agrestis	WSM78 W9 159 15	WSM78 W9 159
P. gregaloides	WSM78 W9 159 16	WSM78 W9 159
M. arvalis/ agrestis	WSM78 W9 159 17	WSM78 W9 159
P. gregaloides	WSM78 W9 159 18	WSM78 W9 159
P. gregaloides	WSM78 W9 159 19	WSM78 W9 159
P. gregaloides	WSM78 W9 159 20	WSM78 W9 159
P. gregaloides	WSM78 W2 27 1	WSM78 W2 27
P. gregaloides	WSM78 W2 27 2	WSM78 W2 27
P. gregaloides	WSM78 W2 27 3	WSM78 W2 27
P. gregaloides	WSM78 W2 27 4	WSM78 W2 27
P. gregaloides	WSM78 W2 27 5	WSM78 W2 27
P. gregaloides	WSM78 W2 27 6	WSM78 W2 27
pi. Arvaloides	WSM78 W2 27 7	WSM78 W2 27
P. gregaloides	WSM78 W2 27 8	WSM78 W2 27
P. gregaloides	WSM78 W2 27 9	WSM78 W2 27
m. oeconomus	WSM78 W2 27 10	WSM78 W2 27
p. arvaloides	WSM78 W2 27 11	WSM78 W2 27
P. gregaloides	WSM78 W2 27 12	WSM78 W2 27
P. gregaloides	WSM78 W2 27 13	WSM78 W2 27
P. gregaloides	WSM78 W2 27 14	WSM78 W2 27
P. gregaloides	WSM78 W2 27 15	WSM78 W2 27
P. gregaloides	WSM78 W2 27 16	WSM78 W2 27
P. gregaloides	WSM78 W2 27 17	WSM78 W2 27
P. gregaloides	WSM78 W2 6 1	WSM78 W2 6
M. arvalis/ agrestis	WSM78 W2 6 2	WSM78 W2 7
P. gregaloides	WSM78 W2 6 3	WSM78 W2 8
M. arvalis/ agrestis	WSM78 W2 6 4	WSM78 W2 9
M. arvalis/ agrestis	WSM78 W2 6 5	WSM78 W2 10
M. arvalis/ agrestis	WSM78 W2 6 6	WSM78 W2 11
P. gregaloides	WSM78 W2 6 7	WSM78 W2 12
p. gregaloides	WSM78 W2 6 8	WSM78 W2 13
P. gregaloides	WSM78 W2 6 9	WSM78 W2 14
P. gregaloides	WSM78 W2 6 10	WSM78 W2 15
M. arvalis/ agrestis	WSM78 W2 6 11	WSM78 W2 16
P. gregaloides	WSM78 W2 6 12	WSM78 W2 17

Species	ID	Stratigraphic level
P. gregaloides	WSM78 W2 6 13	WSM78 W2 18
P. gregaloides	WSM78 W2 6 14	WSM78 W2 19
P. gregaloides	WSM78 W2 6 15	WSM78 W2 20
M. oeconomus	WSM 78 W2 87 2	WSM 78 W2 87 2
M. arvalis/ agrestis	WSM76 W1-A 350/321	WSM76 W1-A 350/321
P. gregaloides	WSM76 W1-A 380/182 1	WSM76 W1-A 380/182 1
M. arvalis/ agrestis	WSM76 W1-A 380/182 2	WSM76 W1-A 380/182 2
M. arvalis/ agrestis	WSM76 W1B 440/210	WSM76 W1B 440/210
P. arvalidens	WSM76 W1-B 450/215 1	WSM76 W1-B 450/215 1
P. arvalidens	WSM76 W1-B 450/215 2	WSM76 W1-B 450/215 2
P. gregaloides	WSM76 W1-B 450/215 3	WSM76 W1-B 450/215 3
M. arvalis/ agrestis	WSM76 W1-B 450/215 4	WSM76 W1-B 450/215 4
M. arvalis/ agrestis	WSM76 W1-B 450/215 5	WSM76 W1-B 450/215 5
P. gregaloides	WSM77 W5 R4 1	WSM77 W5 R4 1
P. gregaloides	WSM77 W5 R4 10	WSM77 W5 R4 10
P. gregaloides	WSM77 W5 R4 11	WSM77 W5 R4 11
P. gregaloides	WSM77 W5 R4 12	WSM77 W5 R4 12
P. gregaloides	WSM77 W5 R4 13	WSM77 W5 R4 13
P. gregaloides	WSM77 W5 R4 14	WSM77 W5 R4 14
P. gregaloides	WSM77 W5 R4 15	WSM77 W5 R4 15
P. gregaloides	WSM77 W5 R4 16	WSM77 W5 R4 16
P. gregaloides	WSM77 W5 R4 17	WSM77 W5 R4 17
P. gregaloides	WSM77 W5 R4 18	WSM77 W5 R4 18
P. gregaloides	WSM77 W5 R4 19	WSM77 W5 R4 19
P. gregaloides	WSM77 W5 R4 2	WSM77 W5 R4 2
P. gregaloides	WSM77 W5 R4 20	WSM77 W5 R4 20
P. gregaloides	WSM77 W5 R4 21	WSM77 W5 R4 21
P. gregaloides	WSM77 W5 R4 22	WSM77 W5 R4 22
P. gregaloides	WSM77 W5 R4 23	WSM77 W5 R4 23
P. gregaloides	WSM77 W5 R4 24	WSM77 W5 R4 24
P. gregaloides	WSM77 W5 R4 25	WSM77 W5 R4 25
P. gregaloides	WSM77 W5 R4 26	WSM77 W5 R4 26
P. gregaloides	WSM77 W5 R4 27	WSM77 W5 R4 27
P. gregaloides	WSM77 W5 R4 28	WSM77 W5 R4 28
P. gregaloides	WSM77 W5 R4 29	WSM77 W5 R4 29
P. gregaloides	WSM77 W5 R4 3	WSM77 W5 R4 3
P. gregaloides	WSM77 W5 R4 30	WSM77 W5 R4 30
P. gregaloides	WSM77 W5 R4 4	
P. gregaloides	WSM77 W5 R4 5	WSM77 W5 R4 5
P. gregaloides	WSM77 W5 R4 6	WSM77 W5 R4 6
P. gregaloides	WSM77 W5 R4 7	WSM77 W5 R4 7
P. gregaloides	WSM77 W5 R4 8	WSM77 W5 R4 8
P. gregaloides	WSM77 W5 R4 9	WSM77 W5 R4 9
M. arvalis/ agrestis	WSM78 W2 30 1	WSM78 W2 30 1

Species	ID	Stratigraphic level
P. gregaloides	WSM78 W2 30 10	WSM78 W2 30 10
P. gregaloides	WSM78 W2 30 11	WSM78 W2 30 11
P. gregaloides	WSM78 W2 30 12	WSM78 W2 30 12
P. gregaloides	WSM78 W2 30 13	WSM78 W2 30 13
P. gregaloides	WSM78 W2 30 14	WSM78 W2 30 14
P. gregaloides	WSM78 W2 30 15	WSM78 W2 30 15
P. gregaloides	WSM78 W2 30 16	WSM78 W2 30 16
M. oeconomus	WSM78 W2 30 17	WSM78 W2 30 17
M. arvalis/ agrestis	WSM78 W2 30 2	WSM78 W2 30 2
M. arvalis/ agrestis	WSM78 W2 30 3	WSM78 W2 30 3
M. arvalis/ agrestis	WSM78 W2 30 4	WSM78 W2 30 4
M. arvalis/ agrestis	WSM78 W2 30 5	WSM78 W2 30 5
M. arvalis/ agrestis	WSM78 W2 30 6	WSM78 W2 30 6
P. gregaloides	WSM78 W2 30 7	WSM78 W2 30 7
P. gregaloides	WSM78 W2 30 8	WSM78 W2 30 8
P. gregaloides	WSM78 W2 30 9	WSM78 W2 30 9
P. gregaloides	WSM78 W2 35 1	WSM78 W2 35 1
P. gregaloides	WSM78 W2 35 10	WSM78 W2 35 10
P. gregaloides	WSM78 W2 35 11	WSM78 W2 35 11
P. gregaloides	WSM78 W2 35 12	WSM78 W2 35 12
P. gregaloides	WSM78 W2 35 13	WSM78 W2 35 13
P. gregaloides	WSM78 W2 35 14	WSM78 W2 35 14
P. gregaloides	WSM78 W2 35 15	WSM78 W2 35 15
P. gregaloides	WSM78 W2 35 16	WSM78 W2 35 16
P. gregaloides	WSM78 W2 35 17	WSM78 W2 35 17
P. gregaloides	WSM78 W2 35 18	WSM78 W2 35 18
P. gregaloides	WSM78 W2 35 19	WSM78 W2 35 19
P. gregaloides	WSM78 W2 35 2	WSM78 W2 35 2
P. gregaloides	WSM78 W2 35 20	WSM78 W2 35 20
P. gregaloides	WSM78 W2 35 21	WSM78 W2 35 21
P. gregaloides	WSM78 W2 35 22	WSM78 W2 35 22
P. gregaloides	WSM78 W2 35 23	WSM78 W2 35 23
P. gregaloides	WSM78 W2 35 24	WSM78 W2 35 24
P. gregaloides	WSM78 W2 35 25	WSM78 W2 35 25
P. gregaloides	WSM78 W2 35 26	WSM78 W2 35 26
P. gregaloides	WSM78 W2 35 27	WSM78 W2 35 27
P. gregaloides	WSM78 W2 35 28	WSM78 W2 35 28
P. gregaloides	WSM78 W2 35 29	WSM78 W2 35 29
P. gregaloides	WSM78 W2 35 3	WSM78 W2 35 3
P. gregaloides	WSM78 W2 35 30	WSM78 W2 35 30
P. gregaloides	WSM78 W2 35 31	WSM78 W2 35 31
P. gregaloides	WSM78 W2 35 32	WSM78 W2 35 32
P. gregaloides	WSM78 W2 35 33	WSM78 W2 35 33
P. gregaloides	WSM78 W2 35 4	WSM78 W2 35 4

Species	ID	Stratigraphic level
P. gregaloides	WSM78 W2 35 5	WSM78 W2 35 5
P. gregaloides	WSM78 W2 35 6	WSM78 W2 35 6
P. gregaloides	WSM78 W2 35 7	WSM78 W2 35 7
P. gregaloides	WSM78 W2 35 8	WSM78 W2 35 8
P. gregaloides	WSM78 W2 35 9	WSM78 W2 35 9
M. Oeconomus	WSM78 W2 37 1	WSM78 W2 37 1
M. oeconomus	WSM78 W2 37 2	WSM78 W2 37 2
M. oeconomus	WSM78 W2 37 3	WSM78 W2 37 3
M. Oeconomus	WSM78 W2 37 4	WSM78 W2 37 4
P. gregaloides	WSM78 W2 41 1	WSM78 W2 41 1
P. arvaloides	WSM78 W2 41 10	WSM78 W2 41 10
P. gregaloides	WSM78 W2 41 11	WSM78 W2 41 11
M. arvalis/ agrestis	WSM78 W2 41 12	WSM78 W2 41 12
M. arvalis/ agrestis	WSM78 W2 41 13	WSM78 W2 41 13
M. arvalis/ agrestis	WSM78 W2 41 14	WSM78 W2 41 14
M. arvalis/ agrestis	WSM78 W2 41 15	WSM78 W2 41 15
M. arvalis/ agrestis	WSM78 W2 41 16	WSM78 W2 41 16
M. oeconomus	WSM78 W2 41 17	WSM78 W2 41 17
M. oeconomus	WSM78 W2 41 18	WSM78 W2 41 18
M. oeconomus	WSM78 W2 41 19	WSM78 W2 41 19
P. gregaloides	WSM78 W2 41 2	WSM78 W2 41 2
P. gregaloides	WSM78 W2 41 3	WSM78 W2 41 3
P. gregaloides	WSM78 W2 41 4	WSM78 W2 41 4
P. gregaloides	WSM78 W2 41 5	WSM78 W2 41 5
P. gregaloides	WSM78 W2 41 6	WSM78 W2 41 6
P. gregaloides	WSM78 W2 41 7	WSM78 W2 41 7
P. gregaloides	WSM78 W2 41 8	WSM78 W2 41 8
P. gregaloides	WSM78 W2 41 9	WSM78 W2 41 9
P arvaloides	WSM78 W2 46 1	WSM78 W2 46 1
P arvaloides	WSM78 W2 46 10	WSM78 W2 46 10
P arvaloides	WSM78 W2 46 11	WSM78 W2 46 11
P arvaloides	WSM78 W2 46 12	WSM78 W2 46 12
P arvaloides	WSM78 W2 46 13	WSM78 W2 46 13
P arvaloides	WSM78 W2 46 14	
P arvaloides	WSM78 W2 46 15	WSM78 W2 46 15
P arvaloides	WSM78 W2 46 16	WSM78 W2 46 16
P arvaloides	WSM78 W2 46 17	WSM78 W2 46 17
P arvaloides	WSM78 W2 46 18	WSM78 W2 46 18
P arvaloides	WSM78 W2 46 19	WSM78 W2 46 19
P arvaloides	WSM78 W2 46 2	WSM78 W2 46 2
P arvaloides	WSM78 W2 46 20	WSM78 W2 46 20
P arvaloides	WSM78 W2 46 21	WSM78 W2 46 21
P arvaloides	WSM78 W2 46 22	WSM78 W2 46 22
P arvaloides	WSM78 W2 46 23	WSM78 W2 46 23

Species	ID	Stratigraphic level
P arvaloides	WSM78 W2 46 24	WSM78 W2 46 24
P arvaloides	WSM78 W2 46 25	WSM78 W2 46 25
P arvaloides	WSM78 W2 46 26	WSM78 W2 46 26
P arvaloides	WSM78 W2 46 3	WSM78 W2 46 3
P arvaloides	WSM78 W2 46 4	WSM78 W2 46 4
P arvaloides	WSM78 W2 46 5	WSM78 W2 46 5
P arvaloides	WSM78 W2 46 6	WSM78 W2 46 6
P arvaloides	WSM78 W2 46 7	WSM78 W2 46 7
P arvaloides	WSM78 W2 46 8	
P arvaloides	WSM78 W2 46 9	WSM78 W2 46 9
M. oeconomus	WSM78 W2 48 1	WSM78 W2 48 1
M. Oeconomus	WSM78 W2 48 10	WSM78 W2 48 10
M. gregalis	WSM78 W2 48 11	WSM78 W2 48 11
M. gregalis	WSM78 W2 48 12	WSM78 W2 48 12
P. gregaloides	WSM78 W2 48 13	WSM78 W2 48 13
P. gregaloides	WSM78 W2 48 14	WSM78 W2 48 14
P. gregaloides	WSM78 W2 48 15	WSM78 W2 48 15
P. gregaloides	WSM78 W2 48 16	WSM78 W2 48 16
P. gregaloides	WSM78 W2 48 17	WSM78 W2 48 17
P. gregaloides	WSM78 W2 48 18	WSM78 W2 48 18
P. gregaloides	WSM78 W2 48 19	WSM78 W2 48 19
M. oeconomus	WSM78 W2 48 2	WSM78 W2 48 2
P. gregaloides	WSM78 W2 48 20	WSM78 W2 48 20
M. gregaloides	WSM78 W2 48 21	WSM78 W2 48 21
P. gregaloides	WSM78 W2 48 22	WSM78 W2 48 22
P. gregaloides	WSM78 W2 48 23	WSM78 W2 48 23
P. gregaloides	WSM78 W2 48 24	WSM78 W2 48 24
P. gregaloides	WSM78 W2 48 25	WSM78 W2 48 25
P. arvarloides	WSM78 W2 48 26	WSM78 W2 48 26
P. arvaloides	WSM78 W2 48 27	WSM78 W2 48 27
P. gregaloides	WSM78 W2 48 28	WSM78 W2 48 28
P. gregaloides	WSM78 W2 48 29	WSM78 W2 48 29
M. oeconomus	WSM78 W2 48 3	WSM78 W2 48 3
P. gregaloides	WSM78 W2 48 30	WSM78 W2 48 30
P. gregaloides	WSM78 W2 48 31	WSM78 W2 48 31
P. gregaloides	WSM78 W2 48 32	WSM78 W2 48 32
P. gregaloides	WSM78 W2 48 33	WSM78 W2 48 33
P. gregaloides	WSM78 W2 48 34	WSM78 W2 48 34
M. oeconomus	WSM78 W2 48 4	WSM78 W2 48 4
M. oeconomus	WSM78 W2 48 5	WSM78 W2 48 5
M. oeconomus	WSM78 W2 48 6	WSM78 W2 48 6
M. oeconomus	WSM78 W2 48 7	WSM78 W2 48 7
M. oeconomus	WSM78 W2 48 8	WSM78 W2 48 8
M. Oeconomus	WSM78 W2 48 9	WSM78 W2 48 9
M. oeconomus	WSM78 W2 49 2	WSM78 W2 49 2

Species	ID	Stratigraphic level
M. oeconomus	WSM78 W2 49 3	WSM78 W2 49 3
M.gregalis	WSM78 W2 55 1	WSM78 W2 55 1
M. oeconomus	WSM78 W2 55 2	WSM78 W2 55 2
M. arvalis/ agrestis	WSM78 W2 55 3	WSM78 W2 55 3
M. arvalis/ agrestis	WSM78 W2 55 4	WSM78 W2 55 4
M. arvalis/ agrestis	WSM78 W2 55 5	WSM78 W2 55 5
M. oeconomus	WSM78 W2 57 1	WSM78 W2 57 1
M. arvalis/ agrestis	WSM78 W2 57 2	WSM78 W2 57 2
M. arvalis/ agrestis	WSM78 W2 57 3	WSM78 W2 57 3
M. arvalis/ agrestis	WSM78 W2 57 4	WSM78 W2 57 4
M. arvalis/ agrestis	WSM78 W2 57 5	WSM78 W2 57 5
M. arvalis/ agrestis	WSM78 W2 57 6	WSM78 W2 57 6
M. Oeconomus	WSM78 W2 65 1	WSM78 W2 65 1
M. oeconomus	WSM78 W2 65 2	WSM78 W2 65 2
M.oeconomus	WSM78 W2 65 3	WSM78 W2 65 3
M.gregalis	WSM78 W2 76 1	WSM78 W2 76 1
M. oeconomus	WSM78 W2 76 2	WSM78 W2 76 2
M. oeconomus	WSM78 W2 76 3	WSM78 W2 76 3
M. oeconomus	WSM78 W2 76 4	WSM78 W2 76 4
M. oeconomus	WSM78 W2 76 5	WSM78 W2 76 5
M. oeconomus	WSM78 W2 78 1	WSM78 W2 78 1
M. oeconomus	WSM78 W2 78 2	WSM78 W2 78 2
M. arvalis/ agrestis	WSM78 W2 88 1	WSM78 W2 88 1
M. arvalis/ agrestis	WSM78 W2 88 2	WSM78 W2 88 2
P. arvalodies1	WSM78 W2 88 3	WSM78 W2 88 3
P. gregaloides	WSM78 W2 88 4	
P. gregaloides	WSM78 W2 88 5	
P. gregaloides	WSM78 W9 111 1	WSM78 W9 111 1
P. arvalodies	WSM78 W9 111 10	WSM78 W9 111 10
M. arvalis/ agrestis #3	WSM78 W9 111 11	WSM78 W9 111 11
M. arvalis/ agrestis #3	WSM78 W9 111 12	WSM78 W9 111 12
M. arvalis/ agrestis #3	WSM78 W9 111 13	WSM78 W9 111 13
P. gregaloides	WSM78 W9 111 2	WSM78 W9 111 2
P. gregaloides	WSM78 W9 111 3	WSM78 W9 111 3
P. gregaloides	WSM78 W9 111 4	WSM78 W9 111 4
P. gregaloides	WSM78 W9 111 5	WSM78 W9 111 5
P. gregaloides	WSM78 W9 111 6	WSM78 W9 111 6
P. gregaloides	WSM78 W9 111 7	WSM78 W9 111 7
P. gregaloides	WSM78 W9 111 8	WSM78 W9 111 8
P. arvalodies	WSM78 W9 111 9	WSM78 W9 111 9
P. arvalodies	WSM79 W2 22 1	WSM79 W2 22 1
P. arvalodies	WSM79 W2 22 2	WSM79 W2 22 2
P. arvalodies	WSM79 W2 22 3	WSM79 W2 22 3

Species	ID	Stratigraphic level
P. gregaloides	WSM79 W2 22 4	WSM79 W2 22 4
P. gregaloides	WSM79 W2 22 5	WSM79 W2 22 5
P.gregaloides	WSM79 W2 22 6	WSM79 W2 22 6
P. gregaloides	WSM79 W2 22 7	WSM79 W2 22 7
M. arvalis/ agrestis	WSM79 W2 22 8	WSM79 W2 22 8
M. gregalis	WSM79 W2 49 1	WSM79 W2 49 1
M. oeconomus	WSM79 W2/9 182 1	WSM79 W2/9 182 1
M. Oeconomus	WSM79 W2/9 182 2	WSM79 W2/9 182 2
M. oeconomus	WSM79 W2/9 182 3	WSM79 W2/9 182 3
P. gregaloides	WSM79 W2/9 206 1	WSM79 W2/9 206 1
P. gregaloides	WSM79 W2/9 206 10	WSM79 W2/9 206 10
P. gregaloides	WSM79 W2/9 206 11	WSM79 W2/9 206 11
P. gregaloides	WSM79 W2/9 206 12	WSM79 W2/9 206 12
P. gregaloides	WSM79 W2/9 206 13	WSM79 W2/9 206 13
P. gregaloides	WSM79 W2/9 206 14	WSM79 W2/9 206 14
P. gregaloides	WSM79 W2/9 206 15	WSM79 W2/9 206 15
M. Oeconomus	WSM79 W2/9 206 16	WSM79 W2/9 206 16
M. arvalis/ agrestis	WSM79 W2/9 206 17	WSM79 W2/9 206 17
M. arvalis/ agrestis	WSM79 W2/9 206 18	WSM79 W2/9 206 18
M. arvalis/ agrestis	WSM79 W2/9 206 19	WSM79 W2/9 206 19
P. gregaloides	WSM79 W2/9 206 2	WSM79 W2/9 206 2
M. arvalis/ agrestis	WSM79 W2/9 206 20	WSM79 W2/9 206 20
M. arvalis/ agrestis	WSM79 W2/9 206 21	WSM79 W2/9 206 21
M. arvalis/ agrestis	WSM79 W2/9 206 22	WSM79 W2/9 206 22
M. arvalis/ agrestis	WSM79 W2/9 206 23	
M. arvalis/ agrestis	WSM79 W2/9 206 24	WSM79 W2/9 206 24
M. arvalis/ agrestis	WSM79 W2/9 206 25	WSM79 W2/9 206 25
M. arvalis/ agrestis	WSM79 W2/9 206 26	WSM79 W2/9 206 26
M. arvalis/ agrestis	WSM79 W2/9 206 27	WSM79 W2/9 206 27
M. arvalis/ agrestis	WSM79 W2/9 206 28	WSM79 W2/9 206 28
M. arvalis/ agrestis	WSM79 W2/9 206 29	WSM79 W2/9 206 29
P. gregaloides	WSM79 W2/9 206 3	WSM79 W2/9 206 3
M. arvalis/ agrestis	WSM79 W2/9 206 30	WSM79 W2/9 206 30
M. arvalis/ agrestis	WSM79 W2/9 206 31	WSM79 W2/9 206 31
P. gregaloides	WSM79 W2/9 206 4	WSM79 W2/9 206 4
P. gregaloides	WSM79 W2/9 206 5	WSM79 W2/9 206 5
P. gregaloides	WSM79 W2/9 206 6	WSM79 W2/9 206 6
P. gregaloides	WSM79 W2/9 206 7	WSM79 W2/9 206 7
P. gregaloides	WSM79 W2/9 206 8	WSM79 W2/9 206 8
P. gregaloides	WSM79 W2/9 206 9	WSM79 W2/9 206 9
M. arvalis/ agrestis	WSM79 W2/9 24 1	WSM79 W2/9 24 1
P. arvalodies	WSM79 W2/9 24 10	WSM79 W2/9 24 10
P. arvalodies	WSM79 W2/9 24 11	WSM79 W2/9 24 11

Species	ID	Stratigraphic level
P. arvalodies	WSM79 W2/9 24 12	WSM79 W2/9 24 12
P. arvalodies	WSM79 W2/9 24 13	WSM79 W2/9 24 13
P. arvalodies	WSM79 W2/9 24 14	WSM79 W2/9 24 14
P. arvalodies	WSM79 W2/9 24 15	WSM79 W2/9 24 15
M. arvalis/ agrestis	WSM79 W2/9 24 2	WSM79 W2/9 24 2
M. arvalis/ agrestis	WSM79 W2/9 24 3	WSM79 W2/9 24 3
M. arvalis/ agrestis	WSM79 W2/9 24 4	WSM79 W2/9 24 4
M. arvalis/ agrestis	WSM79 W2/9 24 5	WSM79 W2/9 24 5
M. arvalis/ agrestis	WSM79 W2/9 24 6	WSM79 W2/9 24 6
M. arvalis/ agrestis	WSM79 W2/9 24 7	WSM79 W2/9 24 7
P. arvalodies	WSM79 W2/9 24 8	WSM79 W2/9 24 8
P. arvalodies	WSM79 W2/9 24 9	WSM79 W2/9 24 9
P. arvalodies	WSM79 W2/9 30 1	WSM79 W2/9 30 1
M. arvalis/ agrestis	WSM79 W2/9 44 1	WSM79 W2/9 44 1
P. arvalodies	WSM79 W2/9 44 2	WSM79 W2/9 44 2
P arvaliodes	WSM79 W2/9 44 3	WSM79 W2/9 44 2
P. aravloides	WSM79 W2/9 44 4	WSM79 W2/9 44 4
P.arvaloides	WSM79 W2/9 44 5	WSM79 W2/9 44 5
M. arvalis/ agrestis	WSM79 W2/9 50 2	WSM79 W2/9 50 2
M. arvalis/ agrestis	WSM79 W2/9 50 3	WSM79 W2/9 50 3
P. arvalodies	WSM79 W2/9 50 4	WSM79 W2/9 50 2
P. arvalodies	WSM79 W2/9 50 5	WSM79 W2/9 50 5
P.arvaliodes	WSM79 W2/9 59 1	WSM79 W2/9 59 1
M. arvalis/ agrestis	WSM79 W2/9 59 10	WSM79 W2/9 59 10
M. arvalis/ agrestis	WSM79 W2/9 59 11	WSM79 W2/9 59 11
M. arvalis/ agrestis	WSM79 W2/9 59 12	WSM79 W2/9 59 12
M. arvalis/ agrestis	WSM79 W2/9 59 13	WSM79 W2/9 59 13
P.arvaliodes	WSM79 W2/9 59 2	WSM79 W2/9 59 2
P.arvaliodes	WSM79 W2/9 59 3	WSM79 W2/9 59 3
P.arvaliodes	WSM79 W2/9 59 4	WSM79 W2/9 59 4
P.arvaliodes	WSM79 W2/9 59 5	WSM79 W2/9 59 5
P.arvaliodes	WSM79 W2/9 59 6	WSM79 W2/9 59 6
P.arvaliodes	WSM79 W2/9 59 7	WSM79 W2/9 59 7
P.arvaliodes	WSM79 W2/9 59 8	WSM79 W2/9 59 8
M. arvalis/ agrestis	WSM79 W2/9 59 9	WSM79 W2/9 59 2
P. arvarloides	WSM79 W2/9 60 1	WSM79 W2/9 60 1
P. arvarloides	WSM79 W2/9 60 2	WSM79 W2/9 60 2
P.gregaloides	WSM79 W2/9 60 3	WSM79 W2/9 60 3
M. arvalis/ agrestis	WSM79 W2/9 60 4	WSM79 W2/9 60 4
M. arvalis/ agrestis	WSM79 W2/9 61 1	WSM79 W2/9 61 1
P. gregaloides	WSM79 W2/9 61 2	WSM79 W2/9 61 2
P. arvaloides	WSM79 W2/9 61 3	WSM79 W2/9 61 3

Species	ID	Stratigraphic level
M. arvalis/ agrestis	WSM79 W2/9 64 1	WSM79 W2/9 64 1
M. arvalis/ agrestis	WSM79 W2/9 64 2	WSM79 W2/9 64 2
P.arvaloides	WSM79 W2/9 64 3	WSM79 W2/9 64 3
P.arvaloides	WSM79 W2/9 64 4	WSM79 W2/9 64 4
P.arvaloides	WSM79 W2/9 64 5	WSM79 W2/9 64 5
P.arvaloides	WSM79 W2/9 64 6	WSM79 W2/9 64 6
P. arvalodies3	WSM79 W2/9 70 1	WSM79 W2/9 70 1
M. arvalis/ agrestis	WSM79 W2/9 70 10	WSM79 W2/9 70 10
P. arvalodies3	WSM79 W2/9 70 2	WSM79 W2/9 70 2
P. arvalodies3	WSM79 W2/9 70 3	WSM79 W2/9 70 3
P. gregaloides	WSM79 W2/9 70 4	WSM79 W2/9 70 4
M. arvalis/ agrestis	WSM79 W2/9 70 5	WSM79 W2/9 70 5
M. arvalis/ agrestis	WSM79 W2/9 70 6	WSM79 W2/9 70 6
M. arvalis/ agrestis	WSM79 W2/9 70 7	WSM79 W2/9 70 7
M. arvalis/ agrestis	WSM79 W2/9 70 8	WSM79 W2/9 70 8
M. arvalis/ agrestis	WSM79 W2/9 70 9	WSM79 W2/9 70 9
M. arvalis/ agrestis	WSM79 W2/9 73 1	WSM79 W2/9 73 1
P. arvalodies7	WSM79 W2/9 73 10	WSM79 W2/9 73 10
P. arvalodies7	WSM79 W2/9 73 11	WSM79 W2/9 73 11
P. arvalodies7	WSM79 W2/9 73 12	WSM79 W2/9 73 12
P. arvalodies7	WSM79 W2/9 73 13	WSM79 W2/9 73 13
M. arvalis/ agrestis	WSM79 W2/9 73 2	WSM79 W2/9 73 2
M. arvalis/ agrestis	WSM79 W2/9 73 3	WSM79 W2/9 73 3
M. arvalis/ agrestis	WSM79 W2/9 73 4	WSM79 W2/9 73 4
M. arvalis/ agrestis	WSM79 W2/9 73 5	WSM79 W29 73 5
P. gregaloides	WSM79 W2/9 73 6	WSM79 W2/9 73 6
P. arvaloides	WSM79 W2/9 73 7	WSM79 W2/9 73 7
P. arvaloides	WSM79 W2/9 73 8	WSM79 W2/9 73 8
P. arvaloides	WSM79 W2/9 73 9	WSM79 W2/9 73 9
M. arvalis/ agrestis	WSM79 W2/9 76 1	WSM79 W2/9 76 1
P. arvalodies3	WSM79 W2/9 76 2	WSM79 W2/9 76 2
M. arvalis/ agrestis	WSM79 W2/9 76 3	WSM79 W2/9 76 3
M. arvalis/ agrestis	WSM79 W2/9 76 4	WSM79 W2/9 76 4
M. arvalis/ agrestis	WSM79 W2/9 76 5	WSM79 W2/9 76 5
M. arvalis/ agrestis	WSM79 W2/9 76 6	WSM79 W2/9 76 6
M. arvalis/ agrestis	WSM79 W2/9 76 7	WSM79 W2/9 76 7
M. arvalis/ agrestis	WSM79 W2/9 76 8	WSM79 W2/9 76 8
M. arvalis/ agrestis	WSM79 W2/9 76 9	WSM79 W2/9 76 9
M. arvalis/ agrestis	WSM79 W2/9 82 1	WSM79 W2/9 82 1
P. gregaloides	WSM79 W2/9 82 2	WSM79 W2/9 82 2
P. arvaloides	WSM80 W2 226 1	WSM80 W2 226 1
M. arvalis/ agrestis	WSM80 W2 226 2	WSM80 W2 226 2
M. arvalis/ agrestis	WSM80 W2 226 4	WSM80 W2 226 4
M. arvalis/ agrestis	WSM80 W2 226 5	WSM80 W2 226 5
M. arvalis/ agrestis	WSM80 W2 226 6	WSM80 W2 226 6